THE STANDARD ERRORS OF CHROMOSOME DISTANCES AND COINCIDENCE[1]

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THE PROBLEM

Many problems in linkage require the comparison of two or more values obtained under different genetic or environic conditions, with the object of determining whether or not the observed differences between these values are "significant." By the term "significant difference" is here meant one of such size that it would be improbable for it to have arisen solely as a result of the random sampling of identical germinal material. For the purpose of such comparisons, then, it is necessary first to know the size of the deviations which random sampling by itself would be likely to cause. This is gauged by means of the "standard error," it being ordinarily true that deviations greater than two or three (according to the standard of certainty) times the standard error are very improbable, as a mere result of random sampling. (The use of the so-called "probable error" merely involves the standard error in somewhat different guise, as the former is ordinarily obtained by multiplying the latter by .6745,—a rather superfluous procedure except in special cases).

It has thus become almost axiomatic, for rigorous workers, that in order to be sure of their ground in the interpretation of their results they must have an idea of the standard errors of the values with which they deal. It is true that often the differences are so obviously decisive

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that great refinements are not necessary, and yet, unless some estimates are made of the "errors" involved, there will be occasions, not infrequent, when the investigator will either run the risk of being led into some serious misinterpretation, or else will fail to reap the full meaning from his results.

The standard error of the simple proportion of "crossovers," or, more accurately, of separations, between two pairs of genes,—as well as the error of a chromosome distance (in $\frac{\text{units}}{100}$) so short that it includes no double or multiple crossovers,—is well known, being determined by the familiar formula $\epsilon_p = \sqrt{\frac{p(1-p)}{n}}$, where ϵ_p is the standard error of the proportion of separations or crossovers, p, and n is the total number of individuals counted. (When p represents percents rather than proportions the formula is $\epsilon_p = \sqrt{\frac{p(100-p)}{n}}$.) But the standard errors of longer map lengths, involving double crossovers, and of the index of double-crossover frequency itself,—coincidence,—have not hitherto been worked out. As these are values just as important, in their way, and as frequently used in theoretical work, as the simple crossover values, it is essential that formulae be available for calculating their standard errors also.

STANDARD ERROR OF A MAP LENGTH

Let us consider first the standard error of a chromosome map, or a section of a map long enough to include double, etc., crossovers, based on a count involving simultaneously all the loci dealt with. The map length is the sum of the percent of crossovers in each of the separate regions; this is evidently the same as (100 times) the quotient formed by dividing the total number of individuals counted into the number of *crossings over* (as distinguished from crossovers,—each double crossover containing 2 crossings over, each triple crossover 3 crossings over, etc.). Thus, the map length of the regions considered is really (100 times) the mean value of the number of crossings over per individual in these regions. Now the standard error of any mean value (m) is equal to the standard deviation of the values of the individuals that go to make up the mean, divided by the square root of the number of such individuals $\left(\epsilon_m = \frac{\sigma}{\sqrt{n}}\right)$

In a given set of data, σ, the standard deviation of the values of the individuals, may be determined by the usual process, which consists of getting the square of the deviation of each individual value from the mean value, averaging these squares, and extracting the square root of this average, thus, $\sigma = \sqrt{\frac{\Sigma(i-m)^2}{n}}$, where m is the mean value, in our case the $\frac{\text{map length}}{100}$ or mean number of crossings over per individual, and i the individual value or number of crossings over in any given individual. This can also be expressed in the form, $\sigma = \sqrt{\Sigma\left(\frac{i^2}{n}\right) - m^2}$.

It follows that $\epsilon_m = \sqrt{\frac{\Sigma\left(\frac{i^2}{n}\right) - m^2}{n}}$.

All that now remains is to find the result of substituting for $\Sigma\left(\frac{i^2}{n}\right)$ in the above formula the values derived from the data. Let s be the proportion of single crossovers in the entire total; in the case of each single crossover the value of i, and i^2, is 1, and the sum of the values $\frac{i^2}{n}$ is therefore s. Let d be the proportion of double crossovers; since each double crossover has a value of 2 for i, and of 4 for i^2, the sum $\left(\frac{i^2}{n}\right)$ for these is $4d$. Similarly, let t be the proportion of triple crossovers, the sum of $\left(\frac{i^2}{n}\right)$ for the triples being $9t$; for the quadruples it is $16q$, and so on. Then, the entire sum, $\Sigma\left(\frac{i^2}{n}\right)$, equals $s+4d+9t+16q\cdots$. But m, the map length, equals $s+2d+3t+4q\cdots$; hence, $\Sigma\left(\frac{i^2}{n}\right) = m+2d+6t+12q\cdots$ (or $m+2.1d+3.2t+4.3q\cdots$). Substituting this value of $\Sigma\left(\frac{i^2}{n}\right)$ in the formula for ϵ_m we have

$$\epsilon_m = \sqrt{\frac{(m+2.1d+3.2t+4.3q\cdots) - m^2}{n}},$$

or

$$\epsilon_m = \sqrt{\frac{m(1-m)+2.1d+3.2t+4.3q\cdots}{n}} \qquad (1)$$

It is evident that where there are no double or multiple crossovers to be considered, this expression reduces to the familiar $\sqrt{\frac{p(1-p)}{n}}$ for the standard error, ϵ_p, of the proportion of separations. The above value for ϵ_m, of course, applies to the mean *proportion* of crossings over, or $\frac{\text{map length}}{100}$, so that the standard error of the map length itself, when the latter is expressed in "chromosome units" or percents of crossings over, rather than in proportions, has a value 100 times that of the above expression. When, therefore, m represents the number of units of map length, and d, t, q, etc., represent the percents rather than the proportions of double, triple, quadruple, etc., crossovers, we have instead the relation

$$\epsilon_m = \sqrt{\frac{m(100-m)+200d+600t+1200q\cdots}{n}} \quad \ldots \quad (1a)$$

The above formulae can also be arrived at by considering the map as the sum of the various component distances,—a, b, c,. . . —and applying the equation for the standard error of a sum,

$$\epsilon_s = \sqrt{\epsilon_a^2+\epsilon_b^2+\epsilon_c^2\cdots+2r_{ab}\epsilon_a\epsilon_b+2r_{ac}\epsilon_a\epsilon_c\cdots+2r_{bc}\epsilon_b\epsilon_c\cdots},$$

where ϵ_a, ϵ_b, ϵ_c, etc., are the standard errors of a, b, c, etc., obtained by the $\sqrt{\frac{p(1-p)}{n}}$ formula, and r_{ab}, r_{ac}, r_{bc}, etc., are the correlations between a and b, a and c, b and c, etc., respectively. These correlations are obtained by the formula $r_{p_1p_2} = \frac{d-p_1p_2}{\sqrt{p_1p_2(1-p_1)(1-p_2)}}$, where d is the proportion of double crossovers, and p_1 and p_2 are the proportions of crossovers in the two respective regions considered.

Of course, the formulae given do not take into account possible errors due to the existence of unobserved double crossovers both of whose loci of crossing over lie between two "adjacent" genes, i. e., within the limits of a region indivisible in the experiment; such errors are caused by the conditions of the experiment, whereas the errors given by the formulae are merely those which would be caused by random sampling under these experimental conditions. Furthermore, the formulae do not take into account variations due to determinate causes other than sampling, such as genetic, "developmental," or environic circumstances that influence either crossing over, or the viability of different classes of offspring. As

such sources of variation are seldom absent except where the strictest attention has been given to genetic homogeneity of the parental material, and identity of age, and when the various experiments have been performed simultaneously, with the same food, etc., it would seem a supererogation to develop the formulae for the error of map length due to random sampling further at present, so as to include the errors of composite maps, formed by the combination of the results of wholly different experiments, involving different genes. The methods for determining the "most probable" value of the map from a combination of experiments with different loci have been worked out by FISHER (1922) and by KELLEY (1923), but the standard error of such a "most probable" map can only be estimated roughly, after numerous experiments have given a basis for judging the usual amount of variation due to "determinate" causes, among the results, for identical loci, of experiments involving different subsidiary loci and different environic conditions.

STANDARD ERROR OF COINCIDENCE

Coincidence is the ratio of the proportion of double crossovers (d) which actually occur in two regions (of "lengths" a and b in $\frac{\text{"units"}}{100}$), to the proportion of double crossovers which would occur there if crossings over in the two regions were independent of one another (the latter value being evidently ab). Thus the value of the coincidence ratio, c, is given by the formula $c=\frac{d}{ab}$.

In calculating the standard error of this ratio we may treat it as the quotient of two proportions, p_1 and p_0, where $p_1=\frac{d}{a}$ and $p_0=\frac{b}{1}$. Then, $c=\frac{p_1}{p_0}$. The numerator, p_1, is the proportion of crossovers in region b which occurs among the an cases having crossing over in region a, and the denominator, p_0, is the proportion of crossovers in region b which occurs in the entire total of n individuals. Thus, we are enabled to use for the standard error of coincidence, the well known close-approximation formula for the standard error of a quotient, which may be stated as follows:

$$\left(\epsilon_{\frac{p_1}{p_0}}\right)=\frac{p_1}{p_0}\sqrt{\left(\frac{\epsilon_{p_0}}{p_0}\right)^2-\left(\frac{\epsilon_{p_1}}{p_1}\right)^2-2r_{p_0p_1}\ \frac{\epsilon_{p_0}}{p_0}\ \frac{\epsilon_{p_1}}{p_1}}$$

(where ϵ represents the standard error, and r the correlation, of the values

given in the respective subscripts). To solve this expression for the present case we must find the values of ϵ_{p_0}, ϵ_{p_1} and $r_{p_0p_1}$, and substitute them in the equation given.

As p_0 is merely a proportion (b) of a fixed total (n) its standard error in random sampling is accurately given by the formula $\epsilon_{p_0} = \sqrt{\frac{p_0(1-p_0)}{n}}$. Somewhat similarly, p_1 is a proportion of the "total" n and its standard error, ϵ_{p_1}, may be taken as $\sqrt{\frac{p_1(1-p_1)}{an}}$. As will be explained later, however, the latter expression is only an approximation to ϵ_{p_1}, since the observed value of an is itself subject to variation. In obtaining the value of $r_{p_0p_1}$, it should be noted that the proportion p_0 is gotten by the inclusion of the individuals that go to form p_1 (the double crossovers), with others (single crossovers in region b), to form a proportion of a larger total (n). The formula for the correlation of two such proportions,—one based on individuals that are also included in the other,—is $r = \frac{n_1}{n_0}\frac{\epsilon_{p_1}}{\epsilon_{p_0}}$, where n_1 is the smaller total, in this case an, out of which p_1 is obtained, and n_0 is the more inclusive total, in which p_0 occurs. In the present case, then, $r_{p_0p_1} = \frac{an\epsilon_{p_1}}{n\epsilon_{p_0}} = \frac{a\epsilon_{p_1}}{\epsilon_{p_0}}$

Substituting, now, the above values of ϵ_{p_0}, ϵ_{p_1}, and $r_{p_0p_1}$ in the formula for the standard error of a quotient and simplifying each term, we obtain $\epsilon_c = c\sqrt{\frac{1-p_0}{p_0n} + \frac{1-p_1}{p_1an} - 2\left(\frac{1-p_1}{p_0n}\right)}$. Next, substituting for p_0 and p_1 their values b and $\frac{d}{a}$:

$$\epsilon_c = c\sqrt{\frac{1-b}{bn} + \frac{a-d}{adn} - \frac{2(a-d)}{abn}}$$

Reducing to common denominator, $\epsilon_c = c\sqrt{\frac{ad(1-b)+b(a-d)-2d(a-d)}{abdn}}$

Simplifying the numerator and rearranging terms,

$$\epsilon_c = c\sqrt{\frac{ab-d(a+b+ab-2d)}{abdn}}.$$

Substituting for $\frac{d}{ab}$ its value c, and for $(a-d)$ and $(b-d)$ the symbols a_s and b_s, respectively, signifying the proportion of *single* crossovers in regions a and b, we have, finally,

$$\epsilon_c = c\sqrt{\frac{1-c(a_s+b_s+ab)}{dn}} \quad \text{(approximately)} \quad \cdots \quad (2)$$

For much work it will be found sufficiently accurate to use in place of this a rougher approximation, derivable from it, as follows:

$$\epsilon_c = c\sqrt{\frac{1-cm}{D}} \quad \text{(approximatelv)}, \quad \cdots \quad (2a)$$

where m is the $\frac{\text{map length}}{100}$ of the regions in question, i. e., $m=a+b$, and $D=dn$, the absolute number of double crossovers.

Another form of formula (2), sometimes more convenient in practice, may be obtained from the expression just preceding (2) by dividing the terms of the numerator into the denominator. We then have:

$$\epsilon_c = c\sqrt{\frac{1}{dn} - \frac{1}{bn} - \frac{1}{an} - \frac{1}{n} + \frac{2c}{n}}.$$

Denoting dn, bn and an by D, B and A, which are the absolute numbers rather than the proportions of double crossovers and of crossovers in regions b and a, respectively, we have:

$$\epsilon_c = c\sqrt{\frac{2c-1}{n} - \frac{1}{A} - \frac{1}{B} + \frac{1}{D}} \quad \text{(approximately)} \quad \cdots \quad (2b)$$

As all these formulae are symmetrical with respect to a and b (that is, the latter may be interchanged without altering the final value) it is evident that the use of $\frac{d}{b}$ as p_1 and of a as p_0 in working out the result would have led to the same expression. Nevertheless, as mentioned previously, even formulae (2) and (2b) are not strictly accurate, first, because the formula used for the standard error of a quotient is only an approximation, though a very close one, and second, because the formula

for ϵ_{p_1} is approximate, since the observed values representing the "total" an are variable.

Where the total out of which a proportion is taken is variable, strict accuracy usually demands the use of H, the harmonic mean of these totals, rather than the arithmetic mean (in our case an), in the place of n in the formula $\epsilon_p = \sqrt{\frac{p(1-p)}{r}}$ Where the actual values of the totals are not available for determining H, the latter may usually be calculated from the arithmetic mean, n, by the approximation formula, $H = n\left(1 - \frac{\sigma_n^2}{n^2}\right)$. Substituting, for our case, an for n and $\sqrt{\frac{an(1-an)}{n}}$ for σ_n, we have $H = an + a - 1$. If this is used in place of an in the formula for ϵ_{p_1}, and the formula for ϵ_c worked out by steps similar to those taken previously, we obtain:

$$\epsilon_c = c\sqrt{\frac{2c-1}{n} + \frac{a}{an+a-1}\left(\frac{1}{d} - \frac{1}{b} - \frac{1}{a} + \frac{1-a}{abn}\right)} \quad \text{(approximately)} \quad (3)$$

This is obviously unsymmetrical with respect to a and b, due to the fact that the formula for H used was only an approximation. In fact, it can be shown that the difference between the value of this expression and that obtained when a and b are interchanged would not infrequently be greater, in cases of the sort dealt with experimentally, than the difference between one of them and the original formula (2). Doubtless a better approximation could be obtained by using the mean of a and b rather than a in the unsymmetrical portions of formula (3). This works out as follows:

$$\epsilon_c = c\sqrt{\frac{2c-1}{n} + \frac{a+b}{(n+1)(a+b)-2}\left(\frac{1}{d} - \frac{1}{a} - \frac{1}{b} + \frac{2-a-b}{2abn}\right)} \quad \text{(approximately)} \quad (3a)$$

The error caused in actual problems by the use of the arithmetic rather than the approximate harmonic mean for an is, however, never more than a few percent of the value of ϵ_c. Such an amount is usually of negligible consequence when standard errors are dealt with, for the latter are ordinarily used for determining in round numbers (or numbers of the accuracy of 2.5) the multiple which a given deviation is of the standard deviation. Hence, there would seldom be reason for employing the unwieldy formula (3) or (3a) rather than (2) or (2a).

In strictest accuracy, ϵ_c is indeterminate, because in reality ϵ_{p_1} is indeterminate. The real harmonic mean, H, of observed values of an, must always be 0, since in a practically negligible proportion of samples an will be 0, and the harmonic mean of any series including 0 must always be 0 also; this in turn would make $\epsilon_{p_1}=0$. It is more correct, however, to consider the deviations of p_1 itself, since the root mean square of these really give ϵ_{p_1}. If we do this, we find that when $an=0$, since the deviation of d also $=0$, the proportion p, being $\frac{d}{an}$, or $\frac{0}{0}$, is indeterminate, and its deviation is therefore indeterminate also. This causes ϵ_{p_1} to be indeterminate, and consequently ϵ_c, even though a sample in which an was 0 would not occur, in ordinary work, once in a billion times (an would be zero about once in 200,000,000,000 times if a represented 5 units and n a total of 500 individuals).

If, then, we use the term standard error in the most rigorously exact sense we see that in the case of coincidence its value cannot be found, and does not, in fact, exist, as a definite quantity. Nevertheless, we can continue to speak of it, and to use one of the above formulae for ϵ_c in our work, and these values will have a practical meaning similar to that of the standard error of other quantities, inasmuch as a random deviation of a certain number of times this ϵ_c will have about the same amount of probability as a random deviation of another quantity which is the same number of times its standard deviation. And the "probable error," as in other cases, will here too be about .6745 times the value taken as representing standard error, provided dn is a reasonably large number. In the case of coincidence, in fact, the "probable error" is really a value of more definite meaning than the standard error, being determinate, and independent of the indeterminate value of $\frac{d}{an}$ for the cases when $an=0$. Usually, however, it would be necessary first to determine ϵ_c as above, before the probable error could be found.

It should also be noted that although ϵ_c, strictly speaking, is indeterminate, the range of indetermination is very small, since for all ordinary values of a and n used the proportion of samples in which $an=0$ is exceedingly minute, and in each of the latter samples, even though $\frac{d}{an}=\frac{0}{0}$, this ratio can never be greater than 1 (nor less than 0), as d can never exceed an. The standard error, then, which involves the sum of

numerous determinate quantities and these few indeterminate quantities of limited value, becomes very narrowly fixed. Theoretically, limits could be assigned to ϵ_c and it would be found that the difference between these limits is utterly negligible compared with the size of ϵ_c itself, or compared with the difference between either of them and the practically adequate value given by approximation formula (2). Thus, the question of the more exact determination of ϵ_c ceases to be of practical moment.

THE USE OF THE STANDARD-ERROR FORMULAE

Errors of observed versus true values

Every one of the formulae mentioned so far, including those for crossovers, map length and coincidence, has given the standard deviation to be observed in a large collection of random samples if the true values (for proportion of crossovers, double crossovers, coincidence, etc.), that is, the values which would be found in an indefinitely large sample of the same material, were those used in the formula. Values resulting from random sampling of this material that deviate from the "true" value by more than two or three times this standard error may then be taken as improbable, since they can be shown to occur infrequently, and when such values are found it is therefore considered probable that they were drawn from material with a true value different from that assumed.

In practice, however, the question usually to be answered is not the above,—what the observed values may be which have the greatest reasonable deviation from a certain assumed true value,—but the converse, that is, what the true values could be which would have as their greatest "reasonable" deviant a certain observed value. We can not answer this question precisely by the simple use of the preceding formulae, since the standard error, given in the formula, of a true value equal to that observed, is not precisely the same as the standard error of a true value differing from that observed by plus or minus two or three times the latter standard error itself. However, the values of these errors are usually sufficiently alike that one may be used in place of the other without serious danger of an erroneous conclusion, unless the absolute number of one or more of the variants involved is extremely small, and it has accordingly been the practice to use such formulae as the above for finding the limits of the true values which observed values may represent, by adding to and subtracting from the latter 2 or 3 times the error given by the formulae. It is as legitimate to do this in the case of the map and co-

incidence formulae as in the case of the other formulae where this is commonly done.

When greater accuracy is desired, it is customary to use a rather cumbersome method of approximation. In this method the observed value is first assumed to be true, and by the aid of a formula like one of those given above, the plus and minus limits of the "reasonably possible" observed values (differing from the former by 2 or 3 times the standard error) are calculated. These are then assumed to be true, and their standard errors are calculated by the same formula. Deviations from the observed value of two or three times these, in the plus or minus direction, respectively, now give the true values to a second approximation. The same process may be repeated as many times as necessary, until the desired degree of accuracy is attained. In the case of coincidence, this procedure would be considerably more difficult and intricate than would appear from the above outline, since the standard error of any true or assumedly true value of coincidence is a function not only of the coincidence itself, and the total number counted, but also of the different classes of crossovers, the values of which vary in partial independence of one another. Just how to take all these variations into account simultaneously is not at present clear.

When we are dealing with the simple proportion of crossovers, however, or any other simple proportion (such as of non-disjunctional exceptions, mutations, etc.), the above approximation method may be replaced by a more direct and exact procedure. Let p_0 be the observed value of the proportion and p_1 and p_2 the respective larger and smaller possible true values which differ from p_0 by a certain number of times, say a times, their own standard error. Then we have $p_1 - p_0 = a\sqrt{\frac{p_1(1-p_1)}{n}}$, and $p_0 - p_2 = a\sqrt{\frac{p_2(1-p_2)}{n}}$. If we solve these equations for p_1 and p_2, respectively, we find that $p_1 = \frac{2np_0 + a^2 + a\sqrt{4np_0(1-p_0)+a^2}}{2(n+a^2)}$ and p_2 equals an expression which is the same as the above except that a minus sign occurs before the term containing the radical. Thus, if we let p_t represent either extreme possible true value, we have

$$p_t = \frac{2np_0 + a^2 \pm a\sqrt{4np_0(1-p_0)+a^2}}{2(n+a^2)} \quad \ldots\ldots \quad (4)$$

where p_0 is the observed value and a the number of times the standard deviation of the possible true value whereby the latter differs from the observed value. This formula does not seem to be well known, but, although somewhat lengthy, it is necessary where exactitude is sought, and it is especially important when pn is a rather small number.

Errors due to causes other than random sampling

A second point which must be kept in mind in the application of any of the formulae above discussed is that they give an idea of the size of such deviations as result from random sampling alone. A deviation greater than that thus indicated would not prove the effectiveness of a given factor or agency in influencing the value studied unless it could be shown that no other variation was possible in the experiment except that due to random sampling and to this agency. This is seldom the case in work on linkage, non-disjunction, and other genetic processes giving irregular ratios, and so the unmodified formulae of random sampling are only applicable in the comparison of experiments in which the strictest attention has been given to uniformity of genetic and other conditions in all respects except those the influence of which it is desired to determine (or those the amount of influence of which is definitely predictable). As GOWEN's (1919) work shows, even in such cases there may be uncontrollable sources of variation making the deviations greater than in random sampling.

Wherever possible, then, statistical tests should be applied to the material, by getting the results of various samples taken under the (supposedly) same conditions, and determining whether or not the deviations of these samples from one another are greater than would be expected of purely random samples. The formula for this test is easy, since the deviations of the values in the samples from the general mean value, when squared, summed and averaged, so as to get the standard deviation of these values, should not differ significantly from the standard error to be expected of the average sample (determined by one of the above formulae, with the use of H, the harmonic mean, as the mean number per sample). Whether the resultant difference is significant may usually be found with sufficient accuracy by the use of the approximate formula for the standard error of a standard deviation, that is, $\frac{\epsilon}{\sqrt{2N}}$ in which ϵ is the calculated standard error of the samples and N is the number of samples. These methods apply alike to problems of map length, coin-

cidence, percent of crossovers, of non-disjunction, etc. Of course a satisfactory agreement of the observed deviations of the samples with the error expected from random sampling is not a sure proof that other sources of variation may not be at work, but a contrary result,—a significant disagreement,—does prove that the unmodified random sampling formulae do not apply.

If, by reason of tests like the above or on account of *a priori* considerations, it is concluded that the random sampling rules are insufficient, there may remain another mode of procedure for determining whether a given condition or set of conditions is exerting a significant influence upon the genetic phenomenon studied, or for determining the amount of such influence. This, however, like the above test, requires that a considerable number of separate samples have been recorded, preferably in both (or all) of the series to be contrasted. The standard deviation of the values of the separate samples from the general mean value is then calculated for all the series taken together, by the same method as used in the tests discussed above, and this standard deviation, σ, divided by the square root of the number of samples (N_1) comprised in a given series, will give the standard error $\left(\frac{\sigma}{\sqrt{N_1}}\right)$ allowed for the mean of this entire series, provided the special controlled agency which differentiates one series from another is ineffective in influencing the genetic process studied. Similarly, $\frac{\sigma}{\sqrt{N_2}}$, the standard error of the mean of the entire second series, composed of N_2 samples, may be obtained. These two quantities can now be used in the familiar formula for the standard error of a difference, where there is no correlation, $\sigma_d = \sqrt{\sigma_1^2 + \sigma_2^2}$, to determine in this case the standard error for the difference of the means of the two entire series. If, then, the actual difference between these means is more than two or three times the latter standard error, it may be concluded that the agency studied has been effective.

This final conclusion will be valid even if there were numerous other agents affecting the genetic process studied, so long as there was no cause other than "chance" to lead these agents to act on the samples of one series rather than the other,—that is, if each sample, independently of every other, were as likely to come under the influence of one or more of these agents as every other sample. For the diversifying influences

of these extraneous factors, uncorrelated with the controlled factor, has been allowed for by taking the observed standard deviations of the samples rather than the errors calculated on the basis of random sampling. But, as before, while a significant difference between the means of the series will thus prove the effectiveness of an agent, the lack of such a difference will not categorically disprove the latter but will merely assign an upper limit to it.

The above method is theoretically applicable no matter whether the value studied be proportion of crossovers, of non-disjunction or other exceptions, map length, coincidence, or anything else. In the case of coincidence, however, since this requires such large numbers in a sample for a single good determination, it is often impracticable to secure large numbers of samples, but the work can usually be divided into a few samples, at least, so that some estimate can be obtained of the amount of variability due to all "extraneous" causes combined. Thus, an idea of the upper limit of such variability may be formed, by which the significance of the differences observed in different series may be gauged.

Where, however, the coincidence values to be compared concern different regions all of which were studied in the same counts, the formulae of random sampling (2, 2a, 2b) are accurately applicable, provided the approximate equality of contrary classes shows that the effects of differential viability are negligible. For in such a case identical genetic, developmental and other environic factors were acting in the formation of the different gametic coincidence ratios, and the only possible sources of difference in the observed coincidences, aside from the effects of random sampling, are those inherent in the behavior of the different regions concerned and selective agents which may cause the adult ratios to differ from the gametic ones.

Comparisons of values

The formula for the standard error of a difference, of course, applies both in cases like those previously discussed, where the differences between means are dealt with, and also in all cases of purely random sampling. Since this process of getting the root sum of two squares must often be performed repeatedly, it is convenient to use a geometric scheme for making the computation (just as in multiplications and divisions we may use the slide rule). For the present calculation the authors find that if a sheet of coordinate paper be used, with the lines numbered by tens, both down and across, and another numbered piece of the paper, in the form of a strip,

be taken as a ruler, sufficient accuracy is attained by reading the distance subtended on the ruler when this is placed diagonally from a point on the upper edge having a numerical value equal to one of the standard deviations to a point along the left vertical edge having a value equal to the other standard deviation. This method, which obviously depends upon a hypotenuse being equal to the root sum of the squares of the sides, has been found to save considerable time and to be far quicker for this purpose than the slide rule.

Not merely the significance of a difference, but also the limits allowed for the intensity or degree of effect produced, are determined by the formula for the standard error of a difference. Intensities of effect are, however, expressed more intelligibly, and are more readily dealt with, by means of the quotients than by the differences of the values found in different series. The formula for the standard error of quotients of uncorrelated quantities in general has been mentioned in the section on coincidence. For the handling of these quotients the reader may be referred to the examples treated in the account of the effect of X rays upon crossing over in Drosophila autosomes (MULLER 1925).

SUMMARY

1. The formula is given (formulae 1 and 1a) for the standard deviation which would result from random sampling in the case of a chromosome map, or section of a map, the loci involved in which are followed simultaneously.

2. It is shown that the standard error of coincidence is not finally determinate, but that ordinarily its value is very narrowly limited. Formulae (2, 2a, 2b, 3, 3a) are presented, that give with various degrees of approximation the standard deviation of coincidence which would occur in random sampling.

3. Cautions to be observed in the use of these and other formulae for the standard deviations caused by random sampling are pointed out. Methods are reviewed for determining the significance of results in case other sources of variation besides random sampling and the possible influence of the factors to be studied unavoidably enter into the experiment.

4. The formula (4) is given for determining the maximum and minimum "possible" true values of a proportion of crossovers or of other genetic types which might, in random sampling, have been represented by a given observed value. This gives results somewhat different from those obtained by the formula in common use for this purpose.

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STUDIES IN TWIN RESEMBLANCE

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PROCEDURE

These studies concern themselves chiefly with the following questions:

(1) Do older twins show a greater degree of similarity than younger twins?

(2) Do like-sex pairs show a greater degree of similarity than unlike-sex pairs?

(3) Do twins show a greater degree of similarity in acquired abilities than in original nature?

(4) Do twins suffer any intellectual handicaps?

(5) Can symmetry reversal in handedness and whorl of head-hair be accepted as evidence of the monozygotic origin of twins?

(6) Do palm patterns offer any certain evidence of the monozygotic origin of twins?

(7) Is there any relationship between left-handedness and twinning?

Two hundred twelve pairs of twins were examined, divided according to sex, as follows:

Boy-boy pairs	71
Girl-girl pairs	78
Boy-girl pairs	63
Total	212

These twins varied in age from 90 months to 238 months and were distributed through the school grades from the third to the twelfth.

THE DATA COLLECTED

The data were all collected in the schools of seventeen cities of southern Wisconsin. To insure a random sampling, careful inquiry was made in each school for all the twins enrolled. In some instances this task was performed by the census officer who compiled a list of twins from his records. This is the best procedure, wherever such records are available. Other investigators have called attention to the fact that unlike-sex twins are likely to be overlooked. The ratio between the number of pairs examined, 71 ab : 63 ax : 78 xy, corresponds fairly well with the accepted ratio. With few exceptions the measurements were all taken by the author, who also did most of the scoring of the test papers. While ideal conditions

Measurements	*Number of pairs*
Terman group test of mental ability	113
National intelligence test	97
Thorndike-McCall reading scale	203
Courtis standard research tests, series B:	
Addition	206
Subtraction	205
Multiplication	200
Division	174
Memory span for digits	210
Discrimination for lines	92
Discrimination for ovals	212
O-test for speed of movement	210
Kansas City hand-writing scale	204
Age	211
Grade	206
Section of grade	206
Height, standing	211
Height, sitting	197
Weight	208
Cephalic index	204
Color of eyes	206
Color of hair	205
Whorl of head-hair	186
Handedness	201
Palm patterns	200

for testing were not usually encountered, the conditions for any given pair of twins did not vary, so that comparisons from the standpoint of similarities may be made with considerable confidence.

Throughout these studies all males are designated by "a" or "b," the first letters of the alphabet; all females are designated by "x" or "y," the last letters of the alphabet. Each pair of twins is given a number and the

individuals of a pair are designated by the letters which denote their sex. Thus, 105-ab means a pair of boys; 217-xy means a pair of girls; while 195-ax means a boy-girl pair, of which 195-a is the boy and 195-x is the girl. The system can easily be extended to include triplets, or any number of multiple births. Thus, 113-xyz in the author's collection means a set of girl triplets. To refer to particular measures, for example, the intelligence quotient (I.Q.) of 113-x is 65; of 113-y, 69; and of 113-z, 76. By this method the identity of the individual is established by the same symbol that indicates his sex, an obviously useful device.

In figuring correlations the PEARSON coefficient was used. In all cases where the range was fairly large, the scattergram method was adopted, but with one modification. Like-sex twins are a special case in which correlations are sought between varying amounts of the same trait in different individuals. Ordinarily, the correlation is figured between different traits in the same individuals. It is customary to figure the correlation, for example, between ability in mathematics and language for any particular group, pairing the scores. But in the case of twins it is desired to know the correlation between the abilities of the pair in mathematics or in language, pairing the individuals. As a consequence, there is no principle to determine the axis upon which a particular member of a twin pair shall be placed. If numbers are drawn in pairs by chance and the smaller is always placed on one axis and the larger on the other, a spurious correlation results. To avoid such an effect each twin was entered twice in the scattergram, once on each axis. As a result the standard deviation of each scale was the same, a compensation in computation for the extra labor involved in the double entry.

In cases where the range of the scale was decidedly limited, as in memory span for digits, and in all cases where unlike-sex pairs of twins were involved, HULL'S modification of the THURSTONE formula was used:

$$r = \frac{(M_{AB}) - (M_A \times M_B)}{\sqrt{M_A^2 - M^2_A} \quad \sqrt{M_B^2 - M^2_B}}$$

where M_A is the mean of one variable and M_B is the mean of the other variable. The deviations are figured from zero. When applied to the special case of like-sex twins, the formula becomes:

$$r_{AB} = \frac{M_{AB} - \left(\frac{M_A + M_B}{2} \times \frac{M_A + M_B}{2}\right)}{\left(\frac{M_A^2 + M_B^2}{2}\right) - \left(\frac{M_A + M_B}{2}\right)^2}$$

To figure correlations between scores and age to derive coefficients for partialing out age, the formula becomes:

$$r_{AC} = \frac{\frac{M_{AC}+M_{BC}}{2} - \left(\frac{M_A+M_B}{2} \times M_C\right)}{\sqrt{\left(\frac{M_A{}^2+M_B{}^2}{2}\right) - \left(\frac{M_A+M_B}{2}\right)^2}\ \sqrt{M_C{}^2-M^2{}_C}}$$

Here, again, there are compensations for the extra labor of the double entry, r_{AC} and r_{BC} being equal. The partial correlation, with age held constant, was then computed by the usual formula. All coefficients of correlation reported in this study are coefficients of partial correlation, age having been held constant.

In all cases of unlike-sex twins, or combinations involving unlike-sex twins, the regular method of computing the PEARSON coefficient was used. Double entry was unnecessary, since sex determined the axis upon which each particular twin should be placed. These coefficients have been calculated twice. One hundred sixteen correlations of zero order were computed on HULL'S correlation machine as a check on the original computations. It is therefore apparent that great care has been exercised to insure accurate results.

This study was inspired by Doctor V. A. C. HENMON of the UNIVERSITY OF WISCONSIN and brought to completion under his direction. Many others have rendered valuable assistance, particularly Doctor CLARK L. HULL, also of the UNIVERSITY OF WISCONSIN, and R. A. FISHER, M.A., chief statistician of ROTHAMSTED EXPERIMENTAL STATION, Harpenden, England. It is perhaps not amiss to acknowledge with gratitude the coöperation of the twins who, with patience and long-suffering, volunteered as subjects for these investigations.

THE IDENTIFICATION OF MONOZYGOTIC TWINS

Direct evidence of the monozygotic origin of twins is supplied by the foetal membranes. WILDER (1904) gives a four-fold grouping of data bearing on the intra-uterine relationships of these membranes. A study of WILDER'S types leads to the impression that it is not possible in every case, owing to the great diversity of conditions, to make an unequivocal classification. NEWMAN (1917) asserts that the presence or absence of more than a single corpus luteum will establish beyond doubt the monozygotic or dizygotic origin of a pair of twins. Since it can only be obtained by operation during pregnancy or by post-mortem examination of the

mother after birth, such evidence is rarely available. A common placenta is also considered as proof of one-egg origin, as is a common chorion. It is apparent, of course, that such evidence can not be secured by anyone except the obstetrician, particularly after the twins have reached school age, the period which lends itself most readily to an extensive investigation. If any practical grouping of twins as to their zygotic origin is to be effected, other evidence must be sought.

Biologists maintain that one-egg twins are always of the same sex. This is due to the fact that sex is determined zygotically at the time of fertilization. The theory states that there are two kinds of sperm and but one kind of egg, and the sex of the individual depends on whether a male-producing or a female-producing sperm fertilizes a particular egg. Therefore, a fertilized egg which twins, can produce individuals of one sex only.

In this connection sex ratios among twins are significant. The problem has been carefully considered by several investigators, notably NEWMAN (1917), COBB (1915) and MERRIMAN (1924). The data are given in table 1.

TABLE 1

Table showing sex ratios among twins.

	AB	AX	XY
Twin population.....	234,497	264,098	219,312
Ratio.....	.88	1.00	.83
Twin population.....	1118	1193	1023
Ratio.....	.93	1.00	.87

The United States Census affords additional data on sex ratios. In 1921 there were reported in the birth-registration area of the United States a total of 20,021 cases of twins of which 38,733 were live births and 1309 were still births, making a total of 40,042 twins. It will be noted by the following tables that the figures approximate the 1 : 1 : 1 ratio more closely than any data heretofore reported.

TABLE 2

Distribution of the number of pairs of twins (including still births in all cases where there was at least one live birth) by sex and color, reported in the birth-registration area of the United States in 1921.

RACE	AB	AX	XY	TOTAL
White.....	5952	6162	5821	17,935
Colored.....	687	736	663	2,086
Total.....	6639	6898	6484	20,021

TABLE 3

Sex ratios of twins, based on table 2.

RACE	AB	AX	XY
White	.97	1.00	.94
Colored	.93	1.00	.90
All cases	.96	1.00	.94

The biological argument is, that if sex is determined at the time of the fertilization of the egg, then there ought to be, by the law of chance, as many twin pairs of unlike sex as of like sex. But the actual facts are that there are twice as many like-sex pairs as unlike-sex pairs. The actual ratio is approximately 1 : 1 : 1 while the theoretical ratio is 1 : 2 : 1. NEWMAN (1917, p. 10) concludes that "the only satisfactory explanation of this discrepancy between the observed and the expected ratios appears to be that *nearly half of all same-sexed twins are monozygotic and hence morphologically stand for but one individual to a pair.*" It follows, then, that about one-fourth of all twin births are of monozygotic origin. MERRIMAN (1924) took the actual ratios instead of the approximate ratio of 1 : 1 : 1 and concluded that the number of monozygotic twins is about three-eighths of the total number of like-sex twins. This, then, is the first clew to the indirect identification of one-egg twins. All twins of unlike sex may be regarded as fraternal; monozygotic twins are found only among like-sex pairs and constitute about three-eighths of that group. While this simplifies the problem somewhat, it leaves the zygotic identification of one-half of the twin population a mystery, since it is just as difficult to say with certainty which twins of the like-sex pairs are monozygotic, as which are dizygotic.

For the identification of one-egg twins other characteristics than those of sex must be sought. Among the most promising of these is what is called symmetry reversal or mirror imaging.

It finds all degrees of expression from complete reversal of stomach, heart and viscera in conjoined twins and double monsters to the mirror-imaging of friction-ridge patterns, reversal in direction of the whorl of the head-hair, and right-handedness in one twin and left-handedness in the other. If twinning is due to fission, as some biologists maintain, symmetry reversal is a condition which may be expected from a developmental standpoint and can therefore be accepted with considerable confidence as evidence of one-egg origin. NEWMAN (1917, p. 152) says,

"The two phenomena [mirror-imaging and polyembryony] are so closely related that it is my belief that the occurrence of symmetry reversal or mirror-imaging in twins or double monsters may safely be taken as a criterion of their monozygotic origin."

It seems natural to expect that the product of a single egg which would ordinarily have produced a single bilaterally symmetrical individual, should show symmetry in its halves. Symmetry reversal in conjoined twins, where there is no doubt of monozygotic origin, is a well-attested fact and there is no reason to suppose that the same phenomenon may not manifest itself in separate one-egg twins.

It has been pointed out by NEWMAN (1917) that, due to intra-uterine hazards, unequal nutrition and inequality in somatic segregation, it is not safe to conclude that lack of similarity in unit characters is absolute evidence of dizygotic origin. It is quite possible that some unlike twins may be duplicates. On the other hand, it is just as probable that some twins which are very similar, even identical in some traits, are not monozygotic. A summation of all the evidence, sex, symmetry reversal, and striking similarities may lead pretty close to the truth. But with our present knowledge of the facts, any grouping of twins as monozygotic or dizygotic, on the basis of indirect evidence, must be largely experimental. Such an experimental grouping might be effected on the following characters:

1. Sex.
2. Symmetry reversal:
   a. Friction-ridge patterns of fingers, palms and soles.
   b. Reversal in direction of the whorl of the head-hair.
   c. Right- and left-handedness.
   d. Birth-marks, moles, freckle patterns, etc.
3. Identity or similarity of physical traits:
   a. Similarity of features.
   b. Texture and coloration of skin.
   c. Color of hair.
   d. Color of eyes.
   e. Height, standing and sitting.
   f. Weigh..
   g. Cephalic index.

SYMMETRY REVERSAL

The phenomenon of symmetry reversal often occurs in conjoined twins. The asymmetry of the unpaired organs of the normal individual in which the greater curvature of the stomach is to the left, the apex of the heart to the left, the aortic arch to the left, and the vena cava to the right, is

completely or partially reversed in one member of the pair. This condition is called "situs inversus viscerum" in contrast to the normal condition which is known as "situs solitus." Numerous instances have been reported and SPAETH and SCHATZ call attention to small deviations often found in separate one-egg twins (NEWMAN 1923).

The whorl of the head-hair (the crown, as it is commonly called) of the normal person is from left to right, or clockwise. It is for this reason that most people part their hair on the left; it naturally falls to the right. It is for the same reason that the mother of the boy whose head-hair whorls to the left has such difficulty in making her young son's hair "stay combed" when she parts it on the left. A slight change in technique would relieve her of her worries. The literature on twins has a few references to reversal of the whorl of the head-hair. NEWMAN (1923) mentions it, as does SANO (1916), but up to the time of this study no attempt seems to have been made to determine the frequency of its occurrence or the variations which the phenomenon manifests.

Sometimes this characteristic can be determined at a glance, especially if the hair is short. More frequently the hair requires considerable combing in order to discover the natural whorl. This is especially true in the case of girls. Long, fine hair sometimes assumes a false whorl but the true whorl can always be located close to the scalp. Double crowns are not unusual. My data reveal thirteen such cases. Occasionally, a sort of composite condition is found which is quite puzzling, but careful examination usually resolves it into two crowns lying very close together. No cases were found in which both members of a pair had double crowns.

One hundred eighty-six pairs of twins were examined to determine the whorl of the head-hair. The frequency of occurrence of this type of symmetry reversal is given in table 4. The plus sign (+) indicates a whorl to the right, or clockwise; the minus (−) sign indicates a whorl to the left, or counter-clockwise. Two signs in a parenthesis indicate a double crown, and the position of the signs indicate their position relative to each other on the head. Thus xy (+) (−+) means a girl-girl pair, the right-hand member of which has a double crown; and of these two crowns, the left-hand crown whorls to the left, the right-hand crown to the right.

As in the case of whorl of the head-hair, no effort seems to have been made, heretofore, to determine the amount of left-handedness among twins, though the condition in which one member of a pair is right-handed and the other left-handed has been recognized as symmetry reversal (NEWMAN 1923). In this study, the type of handedness manifested by any particular member of a pair of twins was determined by questioning, and

TABLE 4

Frequency of occurrence of symmetry reversal in whorl of head-hair in a total number of 186 cases.

TYPE	FREQUENCY BY PAIRS	FREQUENCY BY GROUPS	PERCENT
ab(+) (−)	8		
ab(−) (−)	1		
ab(+) (+−)	2		
ab(−) (+−)	2		
ab(+) (−+)	1		
ab(−) (−+)	0		
ab(+) (++)	0		
ab(−) (++)	0	14	7.53
xy(+) (−)	5		
xy(−) (−)	0		
xy(+) (+−)	2		
xy(−) (+−)	0		
xy(+) (−+)	0		
xy(−) (−+)	0		
xy(+) (++)	0		
xy(−) (++)	0	7	3.76
ax(+) (−)	15		
ax(−) (−)	3		
ax(+) (+−)	5		
ax(−) (+−)	0		
ax(+) (−+)	0		
ax(−) (−+)	0		
ax(+) (++)	1		
ax(−) (++)	0	24	12.90
Total symmetry reversal	45	45	24.19
ab(+) (+)	51	51	27.41
xy(+) (+)	56	56	30.10
ax(+) (+)	34	34	18.27
Total.....	186	186	99.97

sometimes by experiment. Most twins when asked "Are you right- or left-handed?" replied unhesitatingly, "Right." When a twin reported himself as left-handed, he was questioned further. It was discovered that many individuals who are naturally left-handed have learned to write with the right hand, or have made a transfer in many of the fundamental coördinations. To avoid error, therefore, as much as possible, such individuals were further asked, "How do you throw a ball?" or "How do you hold a needle when you sew?" Or the individual was handed a ball and asked to throw it to the examiner. This last method is particularly

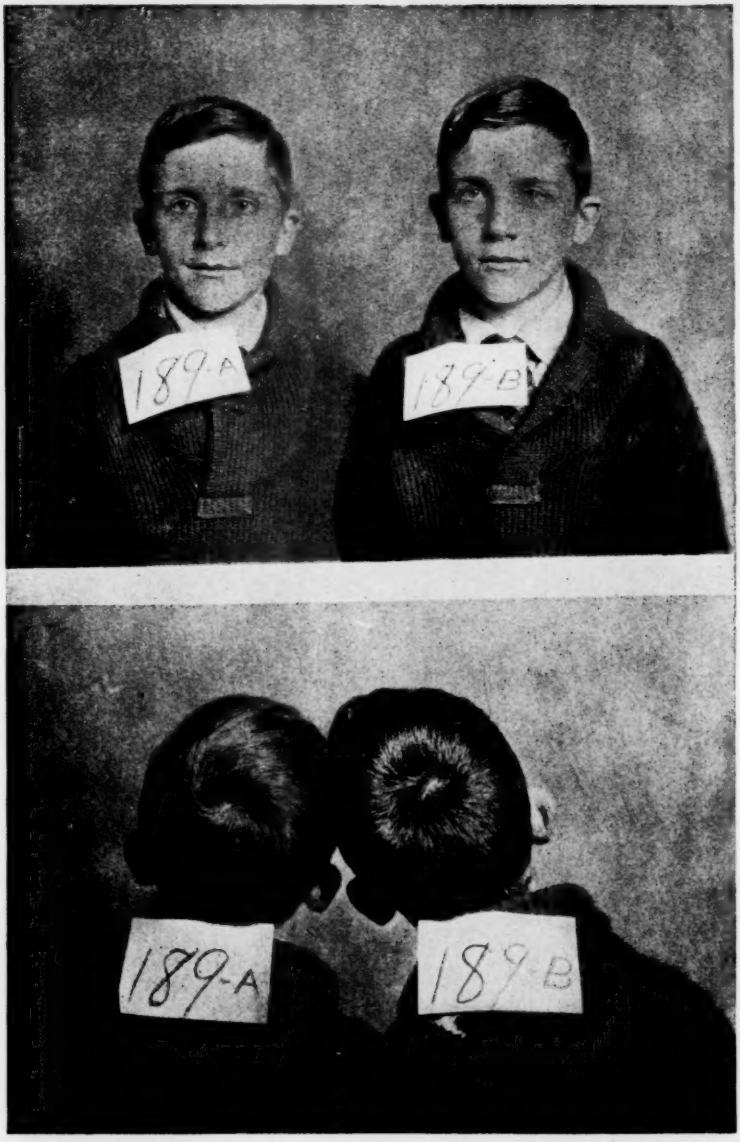
Legend for Plate 1

SYMMETRY REVERSAL IN WHORL OF THE HEAD-HAIR

This is a pair of twin boys who show symmetry reversal in whorl of the head-hair and in handedness. They are eleven years of age and both are in the fourth grade. In height, sitting, "b" is the taller by 4 millimeters, and in weight, the heavier by half a pound. The eyes of both are blue and the hair is a deep chestnut. They have the same intellectual ability. Table 5 below will reveal other resemblances. "a" is fifteen minutes older than his brother. "b" says he was left-handed in childhood but broke his arm about the fourth year. He still chores with the left hand. These twins may be of one-egg origin, but there is no unequivocal evidence of such a genesis.

Table 5

TRAIT	A	B	DIFFERENCE
Age	142 mo	142 mo	None
Grade	4	4	None
Section	2	2	None
Height, sitting	750 mm	754 mm	4 mm
Height, standing	1389 mm	1418 mm	29 mm
Weight	74.5 lb	75.0 lb	0.5 lb
Skull, length	184 mm	191 mm	7 mm
Skull, width	151 mm	149 mm	2 mm
Cephalic index	0.82	0.78	0.04
Color of eyes	Blue	Blue	None
Color of hair	Deep chestnut	Deep chestnut	None
Handedness	Left	Right (?)	Symmetry reversal
Whorl of head-hair	Clockwise	Counter-clock	Symmetry reversal
Main-line formulae	(7.5.5.4) (9.0.5.5)	(8.6.5.4) (11.7.5.5)	
Patterns	(oo oo oo oo xo xx)	(oo oo oo oo xx xx)	
Intelligence quotients	0.75	0.77	0.02
Reading quotients	0.77	0.77	None
Memory for digits	5	5	None
O-test: speed of movement	123	121	2
Handwriting, quality	6.75	7.75	1.00
Handwriting, speed	24	28	4


189-A
189-B
189-A
189-B

useful with small children. In some instances a tendency toward ambidexterity was found.

The frequency with which symmetry reversal in handedness occurs is shown in table 6. The same symbolism is used as in the case of the whorl of the head-hair. The plus sign (+) means right-handedness; the minus sign (−), left-handedness.

TABLE 6

Frequency of occurrence of symmetry reversal in handedness in a total number of 201 cases.

TYPE	FREQUENCY BY PAIRS	FREQUENCY BY GROUPS	PERCENT
ab(+) (−)	15		
ab(−) (−)	0	15	7.46
xy(+) (−)	7		
xy(−) (−)	1	8	3.98
ax(+) (−)	14		
ax(−) (−)	1	15	7.46
Total symmetry reversal	38	38	18.90
ab(+) (+)	54	54	20.86
xy(+) (+)	61	61	30.34
ax(+) (+)	48	48	23.88
Total.....	201	201	99.98

Combining tables 4 and 6 above reveals a surprising frequency of symmetry reversal. Of the 201 pairs of twins examined, 69 pairs, or 34.30 percent, show one or the other type of reversal and 14 pairs or 6.96 percent show both types. Of these 69 pairs, twenty-three are ab or boy pairs; 15 are xy or girl pairs; and 31 are ax or unlike-sex pairs.

While the data show an unexpected frequency of symmetry reversal they also reveal an extraordinarily confusing fact; namely, symmetry reversal in unlike-sex pairs. Some biologists look upon symmetry reversal as evidence of the monozygotic origin of twins. NEWMAN (1917) has expressed the belief that almost any kind of symmetry reversal may be accepted as evidence of monozygotic origin. WILDER has attempted a classification on the basis of symmetry reversal in friction-ridge patterns. But one-egg twins are said to be always of the same sex and here we have 31 pairs of twins of unlike sex which show unmistakable symmetry reversal in handedness and crown, while 14 show both types. The facts force us to the conclusion that symmetry reversal of these two types can

not be accepted as evidence of the monozygotic origin of twins, or else identical twins are frequently of unlike sex.

These apparently irreconcilable facts tempt to speculation. If monozygotic twins are always of the same sex, can we find an explanation of symmetry reversal in unlike-sex pairs?

Let us take a specific case, pair 158-ax, in which a, the boy, is right-handed and x, the girl, is left-handed. The probabilities are that two eggs were fertilized, one of which produced a, the other, x. The a-egg developed naturally into a normal right-handed boy. The x-egg, however, was retarded in its development, either by the presence of the contemporaneously fertilized a-egg or some other cause, and lost its axiate organization, becoming potentially an egg which would have produced a pair of monozygotic female twins. The a- and the x-eggs at this stage of development represent a set of triplets in which a is fraternal to x and y, x and y being duplicate to each other, that is, pair 158-ax becomes 158-axy. But for some unknown reason, during the course of early development, the right-hand axis of the x-egg degenerated and lost its potency while the left-hand axis reached maturity. The result is a surviving axis which shows symmetry reversal, not to the a-egg, but to the suppressed axis of the x-egg. The result is clearly a case of fraternal twins of the ax type showing symmetry reversal.

Any number of combinations of this sort are possible, and the suggestion goes far to explain what otherwise seem to be contradictory facts. Pair 115-ab is an interesting case, a being an ambidextrous boy with a double crown, one whorling to the right, the other to the left; while b is a normal right-handed boy with a single crown whorling to the right. Judging by the symmetry reversal manifested, a and b should be monozygotic. But note the summary of the measures of the pair, as given in table 7. In my opinion, nearly all the available evidence, both mental and physical, indicates a dizygotic origin. The differences are quite striking, particularly in progress in school, height sitting, weight, skull measurements, intelligence and reading quotients, palmar main-line formulae and patterns. While similarities and differences can not be accepted as proof of either the monozygotic or dizygotic origin of twins, the probabilities are that pair 115-ab represents two contemporaneously fertilized eggs, the b-egg developing into a normal boy, right-handed with a single crown; while the a-egg lost its axiate organization and became potentially a pair of monozygotic twins. But at a later stage the whole egg regained its single axiate organization, the only evidence of the disorganization remaining being the ambidexterity of a and his double crown. Thus, a represents two

axes, one of which shows symmetry reversal to the other and only incidentally to the b-egg.

The suggestion leads to many complex combinations, but this is exactly what is needed to explain the variable facts which the problem presents. There are in my collection, data on a set of triplets, 113-xyz, of which z is undoubtedly fraternal to x and y. This conclusion is justified both by the circumstances of birth and by the physical and mental measurements.

TABLE 7

Measurements of a pair of boy twins showing symmetry reversal in whorl of the head-hair and handedness.

TRAIT	A	B	DIFFERENCE
Age	16 yr	16 yr	None
Grade	10 high	9 high	1 year
Height, standing	171.7 cm	174.4 cm	2.7 cm
Height, sitting	86.9 cm	91.4 cm	4.5 cm
Weight	126.75 lb	175.25 lb	48.5 lb
Skull, length	19.8 cm	20.3 cm	0.5 cm
Skull, width	15.3 cm	14.9 cm	0.4 cm
Cephalic index	0.772	0.733	0.039
Color of eyes	Light brown	Light brown	None
Color of hair	Deep chestnut	Chestnut-black	Some
Crown	(+−)	(+)	Symmetry reversal
Handedness	Left	Right	Symmetry reversal
Palm formulae	(11.9.7.5) (11.9.7.5.)	(10.8.6.3) (7.9.7.5)	Considerable
Palm patterns	(oo oo oo xx oo rr)	(xx xx rr ox xx rr)	Marked
Intelligence quotient	0.86	0.75	0.11
Reading quotient	0.71	0.61	0.10
Arithmetic, accuracy	29	28	1
Arithmetic, speed	36	39	3
Memory digits	6	8	2
Speed of movement	144	72	72
Discrimination of ovals	0.834	0.700	0.13
Handwriting, quality	9.50	8.25	1.25
Handwriting, speed	88	64	22

Z was born first, while x and y followed together shortly after. Z, when examined, was a sophomore in high school; while x and y had dropped out of school in the eighth grade. Z seems to be normal physically, and well developed; x and y are extremely nervous, and dependent upon z in all their activities. Quoting from my notes, "z took the attitude of a mother toward the other two, answered questions for them and gave them instructions." But the most interesting fact is that x and y show no symmetry reversal in either handedness or crown while z is left-handed and her crown whorls to the left. Do we have here what was at one stage of

development potentially a set of quadruplets derived from two eggs, z being the only surviving axis of one of the eggs?

The intimate relationship between left-handedness and twinning has been mentioned by DANFORTH (1919, p. 400) who says, "Rather a surprising number of twin pairs seem to be composed of one right- and one left-handed individual." My data show that at least 19 percent of all twin pairs are composed of a right- and a left-hander. The probabilities are that the percentage is much larger for the reason that the method of examination would fail to take account of transfers. As indicated before, an attempt was made to determine native left-handedness by requiring the execution of some complex coördination like throwing a ball or holding a needle while sewing; but to ascertain the actual amount of left-handedness among twins, some more scientific method is essential.

JONES (1918) made a study of handedness based on physical measurements. His conclusions are based on data secured from a total of 20,000 pairs of arms, half a dozen cadavers and a dozen unpieced skeletons. He found that the bones of the major arm, that is, the bones of the left arm of a native left-hander are larger than the bones of the right arm, and *vice versa*. Transfers can be determined by measuring the muscle swell of the biceps and the fore-arm. An investigation needs to be made by such a method to determine the actual amount of left-handedness among twins.

The intimate relationship between left-handedness and twinning is also revealed by other inquiries which I have just begun. For example, x is a right-handed female twin who married and gave birth to a girl with a crown which whorled to the left, who in turn gave birth to a left-handed daughter. This daughter bore seven children, 4 boys and 3 girls, of whom one boy is left-handed and one has a double crown; and one girl is left-handed. Twin y, the sister of x, bore a left-handed daughter. These genealogies are represented in figure 1 in the symbols used by JORDAN (1911):

represents a right-handed male

represents a left-handed male

represents a right-handed female

represents a left-handed female

The crowns are represented by plus (+) and minus (−) signs, the former indicating a whorl to the right; the latter a whorl to the left; two signs

together indicate a double crown. While incomplete, these genealogies are extremely suggestive.

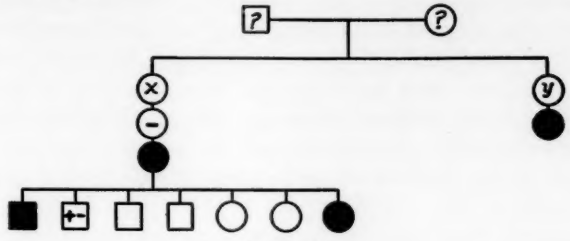


FIGURE 1

A similar case is found in figure 2, where x is a right-handed twin who gave birth to two boys and one girl, one boy being normal as far as handedness and crown are concerned, the other boy having a double crown, the girl being left-handed. The boy with a double crown is unmarried; the normal boy has three children, among whom is a left-handed boy. A fascinating field of investigation, which I think has never before been explored, is opened up here and holds promise of revealing facts which may shed considerable light on left-handedness and twinning.

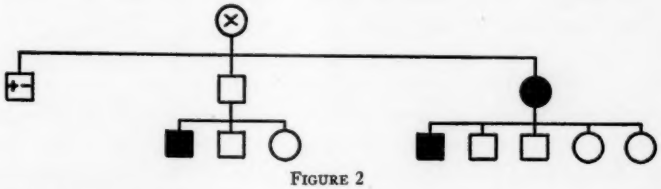


FIGURE 2

JORDAN (1911, p. 20) says

"... inveterate left-handedness is invariably associated with general left-sidedness, i.e., left-leggedness, left eyedness, etc., ... and ... the cerebral localization of this function (i.e., movement of the left hand) in the sinistro-manual is in the right cerebral hemisphere (next BROCA's center in the third frontal convolution), the reverse condition obtaining in the dextro-manual."

It is also significant that HYRTL (1871) reports situs inversus viscerum, particularly of the vascular system, in left-handed individuals. Here, we have exactly the condition so frequently reported among double monsters and conjoined twins.

The frequency of left-handedness among twins, its occurrence in twin-bearing families, and its apparent relationship to situs inversus viscerum, suggest that the fundamental causes of twinning and left-handedness are the same. Is it not quite possible that we have in the left-handed indi-

vidual of a single birth the surviving axis of a bi-axiate egg which might have produced twins had not one axis been suppressed? Such an explanation, it seems to me, would clear up much of the mystery which surrounds the peculiar organization of the neural system of left-handed people.

JONES (1918) reports 4 percent of the population as natively left-handed. His data must have included measurements of some twins, though such a fact is nowhere indicated. If this 4 percent of the population represents in each case the surviving left axis of a bi-axiate egg, then by the law of chance there should be an equal number of individuals who represent the surviving right axes of bi-axiate eggs in which the left axis has degenerated. There is no way of identifying these individuals. But the total number of individuals who are the product of such development is therefore probably 8 percent, twice the number of left-handed individuals. If we add to this the 2 percent of the population who are twins, we have in the general population a total of 10 percent of potential twinning. Or perhaps it would be better to say that in 10 percent of the population the same causes operate to interfere with the normal development of the fertilized egg and the consequent neural organization of the individual. Incidentally, it is interesting to note that of the total number of 793 left-handed individuals examined by JONES, 498 are males and 295 are females, or in terms of percentage, 63 percent are males and 37 percent females. Of the forty left-handed twins examined by myself 23, or 58 percent are males; 13, or 42 percent, are females. These figures reveal a consistent preponderance of males in both cases.

JONES's figures and my own furnish data upon which the correlation between left-handedness and twinning can be reckoned. The United States Census for 1921 reports a total number of live births in the birth-registration area of 1,714,261 and a total number of live births from twin labors of 38,733.[1] According to these figures, the number of twins in each hundred of the population is 2.25, or as DAVENPORT (1920, p. 123) reports, "the average proportion of labors which are twin labors is 1.1 percent for the population as a whole," that is, 2.2 twins in every 101 of the total number of children born. Bearing in mind that JONES reports 4 percent of the population left-handed and that my data show 10 percent

[1] Calculations must be based on total live births, since figures of the number of still births for white and colored populations separately are not available. This causes a slight error augmented somewhat by the fact that the number of live births in twin labors includes "still births in all cases where there was at least one live birth." (Bureau of the Census, Birth Statistics, Seventh Annual Report, 1921.)

of the twin population left-handed, we can set up a four-fold table (table 8).

It has been noted by LOMBROSO that considerable left-handedness exists among lunatics and criminals,—swindlers, murderers and ravishers. It would be extremely interesting to know whether twins contribute to

TABLE 8

Four-fold table showing degree of relationship between left-handedness and twinning.

	Number left-handed per 1000 population	Number right-handed per 1000 population	Totals
Number of twins per 1000 population	a 2.2	b 19.8	22
Number not twins per 1000 population	c 37.8	d 940.2	978
Totals	40.0	960.0	1000

$$r = \cos\left(\frac{\sqrt{bc}}{\sqrt{ad}\ \sqrt{bc}}\right)180^\circ \quad r = .437 \pm .034$$

criminality or not and to what extent. The available data seem to indicate that there may be a relationship between a disturbed organization of the nervous system and moral lapses.

It should be noted that symmetry reversal of handedness and crown occur in only about 34 percent of the twin population. There may not always be such clear evidence of disturbance of the neural organization, but the probabilities are that we are not yet in possession of all of the

facts which might indicate such a deranged condition. Almost 25 percent of the twins examined showed reversal of the whorl of the head-hair and it may be that this type of symmetry reversal has the same significance as left-handedness, namely, some disturbance of the organization of the nervous system. The data show that some twins manifest no symmetry reversal of the type under discussion; that some manifest one type or the other; and that some manifest both types. There may be other kinds of reversal, or less degrees of reversal, which we do not yet recognize.

Certain facts stand out clearly:

1. Symmetry reversal in handedness and whorl of the head-hair cannot be accepted as evidence of the monozygotic origin of twins, assuming that such twins are of like sex.

2. Left-handedness and reversal of the whorl of the head-hair are intimately associated with human twinning.

The evidence suggests the very probable existence of certain other facts:

1. The causes which operate to produce twins probably also operate to produce left-handed individuals.

2. These causes affect about ten percent of the population.

PALM PATTERNS

The collection of the friction-ridge patterns of the palms of about two hundred twins examined during this study was made possible through the application of an inkless method of finger printing developed by Dr. J. H. MATHEWS, Professor of Chemistry at the UNIVERSITY OF WISCONSIN. The method consists in soaking blotter paper in a chemical solution until the blotter is thoroughly impregnated. The blotter is then removed from the tray and the palm pressed firmly upon it so that the solution adheres to the friction ridges. The palm is then placed momentarily upon photographic paper and the result is a beautiful print of the friction ridge patterns. The print is fixed in "hypo" like any ordinary photographic print. The prints illustrated in this study were produced by this method. With materials handy and an assistant to number the prints, an operator can average about a pair of palms a minute. Since the formula leaves no residue on the hands of the subject and since it is not "mussy" it has many advantages over the ink method of printing. While the method had not been worked out in detail at the time of this study, it served the purpose so admirably that it is to be hoped that Doctor MATHEWS will bring it to perfection, if not for commercial purposes, at least for scientific purposes.

The method of classification used is that of WILDER (1916), with one deviation. WILDER uses a small "x" to denote the *absence* of a line. But in view of the fact that in designating patterns the "x" is used to indicate the *presence* of a pattern, it seems less confusing to use the "o" throughout to indicate *absence* and the "x" to indicate *presence*. This is consistent with the method used in plantar designations where the "o" stands for "open field."

The purpose of this study in palm patterns was to distinguish the monozygotic twins from the dizygotic on the basis of identical or at least similar characteristics and mirror-imaging. WILDER (1916) has made such attempts but has met with indifferent success. NEWMAN (1917, p. 157) says,

> "It must not be lost sight of, however, that identity in friction-ridge patterns of twins makes their monozygotic origin highly probable. Identity may demonstrate monozygotic origin, but lack of identity does not disprove the possibility of monozygotic origin."

It would seem, then, that while not all monozygotic twins could be distinguished by similarities in palm patterns, a goodly number could be thus identified.

Naturally the most interesting group of patterns is that of the twins showing symmetry reversal in handedness and whorl of the head-hair. Table 12 gives the main-line formulae and the patterns for fifty-one pairs of this group, and in addition, the same data for twenty-three like-sex pairs which do not show symmetry reversal in handedness or crown. Probably the first fact to strike the student who studies this table is the frequent occurrence of one aberrant pattern. In many instances where three palms show identical or very similar main-line formulae, the fourth shows a marked variation. WILDER (1916) noted this in his studies and was much puzzled to find an aberrant plantar pattern in the case of Mary, one of the pair of conjoined twins. NEWMAN (1917, p. 157) attributes this phenomenon to somatic segregation:

> "In certain monozygotic human twins it might readily happen that by somatic segregation the paternal condition of friction ridges would go to one individual and the maternal to the other, or there might be a partial segregation of important elements of the pattern so that they would be distributed differently in the two."

Whatever the cause, the variation is of relatively frequent occurrence in the main-line formulae of the palms. Instances will be noted in 103-ab, 160-ab, 229-ab, 275-ab, 296-ab; 171-xy, 183-xy, 185-xy, 279-xy; 198-ax, 222-ax; 150-ab, 214-ab, 107-xy, 177-xy, 183-xy. While the difference is

LEGEND FOR PLATE 2

DISSIMILARITY IN PALM PATTERNS

These prints are of a pair of boy twins showing symmetry reversal in whorl of head-hair, the crown of "a" whorling counter-clockwise. Their palms show striking variations, particularly in the thenar and the first interdigital patterns of "b." NEWMAN (1917, p. 157) suggests that such a condition is due to somatic segregation, one twin inheriting the paternal condition of friction-ridge patterns, the other, the maternal.

sometimes comparatively slight, at other times it is considerable. Furthermore, the phenomenon occurs in all groups. A study of the patterns reveals a similar condition. Striking instances are seen in 229-ab, 183-xy, 185-xy, 222-ax. Slight variations occur more frequently. Of course, variations in palm patterns are to be expected with variations in main-line formulae, since the 2nd, 3rd and 4th interdigital patterns are usually determined by the main lines.

But suppose we try to pick out the one-egg twins. Let us take the case of E and L. The formulae for the palms are:

E, (11.0.7.5) (11.0.7.5) (oo oo oo oo oo xx)

L, (11.0.7.5) (11.0.7.5) (oo oo oo oo oo xx)

Here there is complete identity in main-line formulae and patterns. Shall we say that these twins are monozygotic? Before making a decision let us examine other evidence:

TABLE 9

The measurements of twins E and L.

THE TRAIT MEASURED	E	L	DIFFERENCE
Age	172 mo	172 mo	None
Grade	9 Low	9 Low	None
Height, standing	140.5 cm	139.7 cm	0.8 cm
Height, sitting	70.2 cm	69.6 cm	0.6 cm
Weight	67.50 lb	70.25 lb	2.75 lb
Skull, length	17.7 cm	17.8 cm	0.1 cm
Skull, width	14.2 cm	14.5 cm	0.3 cm
Cephalic index	0.802	0.814	0.012
Color of eyes	Light brown	Light brown	None
Color of hair	Deep chestnut	Deep chestnut	None
Handedness	+	+	None
Whorl of head-hair	+	+	None
Intelligence quotient	0.97	0.93	0.04
Reading quotient	1.15	1.22	0.07
Arithmetic, speed	66	58	8
Arithmetic, accuracy	42	44	2
Memory for digits	7	8	1
Discrimination of lines	18	14	4
Discrimination of ovals	0.650	0.884	0.234
O-test	138	122	16
Handwriting, speed	91	82	9
Handwriting, quality	12.5	12.0	0.5

In addition to this evidence, my notes, taken at the time of the examination, say, "Hands alike. Teeth, nose, texture of skin, coloration, eyebrows, same. *Identical.*" Are these twins identical?

Let us take another case of twins, that of P and V. Their main-line formulae and their patterns are:

P, (7.5.5.4) (7.5.5.5) (oo oo oo oo xx xx)

V, (7.5.5.4) (7.5.5.4) (oo oo oo oo xx xx)

There is enough asymmetry here to permit us to say that there is symmetry reversal in main-line formulae. The patterns are identical except in minutiae. Besides, V is left-handed and has a double crown (− +). A study of physical and mental traits likewise shows striking similarity:

TABLE 10

The measurements of twins P and V.

THE TRAIT MEASURED	P	V	DIFFERENCE
Age	119 mo	119 mo	None
Grade	4 low	4 low	None
Height, standing	127.1 cm	129.5 cm	2.4 cm
Height, sitting	70.4 cm	69.8 cm	0.6 cm
Weight	62.50 lb	56.00 lb	6.50 lb
Skull, length	18.1 cm	17.7 cm	0.4 cm
Skull, width	14.7 cm	14.1 cm	0.6 cm
Cephalic index	0.812	0.796	0.016
Color of eyes	Light brown	Light brown	None
Color of hair	Deep chestnut	Medium chestnut	Slight
Handedness	+	−	Symmetry reversal
Whorl of head-hair	+	− +	Symmetry reversal
Intelligence quotient	1.00	0.97	0.03
Reading quotient	0.95	1.02	0.07
Arithmetic, speed	14	16	2
Arithmetic, accuracy	2	1	1
Memory for digits	6	5	1
O-test	102	54	58
Discrimination of ovals	0.484	0.317	0.167
Handwriting, speed	33	57	24
Handwriting, quality	7	7	None

Perhaps the most significant differences are found in skull measurements, but even here the difference in cephalic index is not great. There is a slight difference in color of hair. In speed of movement the difference is marked; likewise in handwriting speed, though the difference is reversed. In quality of handwriting, the scale shows no difference.

That differences in physical traits must not be taken as conclusive evidence that any particular pair of twins is dizygotic, is pointed out by NEWMAN (1917, p. 162),

"It should be pointed out, however, that fairly marked dimensional *differences*, even at birth, could not be used as evidence against the monozygotic

origin of any particular pair of twins; in the armadillo, where the monozygotic origin is specific and unequivocal, there is frequently found a striking difference among the quadruplets of a given set. On the whole, then, it would seem inadvisable to use dimensional measurements, either at birth or in later life, as data for determining the degree of resemblance (coefficient of correlation) between twins."

Further on he says, (p. 171), speaking specifically of friction-ridge patterns,

"In the light of what I have found in armadillo quadruplets, which are unquestionably monozygotic, it does not seem safe to exclude from the category of monozygotic twins those that fail to show identity of pattern; the same practice, if applied to armadillo quadruplets, would lead to grave errors. It is probably safer to say that some monozygotic human twins, like some sets of armadillo quadruplets, are nearly identical, while others, like various quadruplet sets, may differ materially from each other."

In view of the symmetry reversal manifested in twins P and V, the remarkable correspondence in palm patterns, and assuming that differences in physical traits are not necessarily evidence disproving the monozygotic origin of any particular pair of twins, one is tempted to conclude that P and V are monozygotic.

TABLE 11

The measurements of twins A and C.

THE TRAIT MEASURED	A	C	DIFFERENCE
Age	116 mo	116 mo	None
Grade	4 low	4 low	None
Height, standing	114.8 cm	121.2 cm	6.4 cm
Height, sitting	64.8 cm	68.0 cm	3.2 cm
Weight	47.00 lb	53.25 lb	6.25 lb
Skull, length	18.1 cm	18.1 cm	None
Skull, width	14.5 cm	14.5 cm	None
Cephalic index	0.801	0.801	None
Color of eyes	Dark brown	Blue	Marked
Color of hair	Chestnut black	Light chestnut	Marked
Handedness	+	−	Symmetry reversal
Whorl of head-hair	+	+−	Symmetry reversal
Intelligence quotient	0.91	1.03	0.12
Reading quotient	0.76	0.91	0.15
Arithmetic, speed	25	21	4
Arithmetic, accuracy	17	9	8
Memory for digits	6	7	1
Discrimination of ovals	0.40	0.00	0.40
O-test	83	62	21
Handwriting, speed	44	39	5
Handwriting, quality	9.5	10.25	0.75

Legend for Plate 3

IDENTICAL PALMS IN UNLIKE-SEX TWINS

An examination of these patterns reveals that they are almost identical. There is the characteristic suppression of line C in each palm and symmetry reversal, finger for finger, except in the thumbs. In fact, the only marked difference is in the apical pattern of the thumbs. These twins also show symmetry reversal, "x" having a double crown (+ −) and being left-handed. ***But these twins are of unlike sex.*** The case clearly shows that any zygotic classification of twins on the basis of either palm patterns or symmetry reversal is an extremely uncertain procedure. These are the prints of Anthony and Charlotte, 232-ax.

But before we make our decision let us examine another pair of twins, A and C. Their main-line formulae and their patterns are:

A, (11.0.7.5) (11.0.7.5) (oo oo oo oo oo rr)

C, (11.0.7.5) (11.0.7.5) (oo oo oo oo oo rr)

This striking correspondence extends as well to the apical patterns of the fingers (see plate 3), there being almost perfect symmetry reversal, finger for finger, except the thumbs. Not only do we have identical formulae and patterns, but we have also symmetry reversal in handedness, C, the left-handed twin, having also a double crown (+ −). The evidence of physical and mental measurement may also favor the theory of one-egg origin: We have some marked differences here, notably in color of eyes and hair, but we have complete correspondence in skull measurements. We have, to offset the differences in physical traits, four instances of symmetry reversal, in handedness, in crown, and in both palms. Are A and C monozygotic?

We have here, as far as palms are concerned, a case identical with the conjoined twins, Mary and Margaret, reported by WILDER (1916). The palms of all four hands are practically alike in pattern, and it may not, therefore, be correct to speak of mirror-imaging in this connection. NEWMAN (1917, p. 164) says of the case: "Since there is no asymmetry in the hands, there is no chance to observe symmetry reversal or mirror-imaging."

It seems to me, on the face of the evidence presented, that it is at least very probable that these three pairs of twins are identical. The evidence of the palm patterns alone seems to be perfectly clear. Add to this the evidence of symmetry reversal and reasonable similarity in physical and mental traits, the conclusion, in view of the theories which have been urged, is almost unavoidable that E and L, P and V, and A and C are monozygotic twins. This would certainly be my conclusion were it not for one fact which has not been considered. P (Paul) and V (Vivian) and A (Anthony) and C (Charlotte) are unlike-sex twins. E (Eleanore) and L (Lucille) are a pair of girl twins. Their numbers are respectively 155-ax, 232-ax and 274-xy. This does not mean, of course, that pair 274-xy is not monozygotic. This may be a pair of one-egg twins. But such a statement could be made on the basis of sex alone. If unlike-sex twins can be so misleading, may not like-sex pairs be even more so? It is evident that a classification of twins as monozygotic or dizygotic on the basis of palm patterns, or even a summation of evidence, may lead to very grave errors.

TABLE 12

Showing symmetry reversal in handedness and crown, and the main-line and palm-pattern formulae of 74 pairs of twins.

NUMBER	HAND	CROWN	MAIN LINES		PATTERNS
103 a	+	+	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo rr)
b	−	−	(11.8.7.5)	(11.9.7.5)	(oo oo oo ox oo rr)
115 a	−	+−	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo rr)
b	+	+	(10.8.6.3)	(7.9.7.5)	(xx xx rr ox xx rr)
140 a	−	+	(7.5.5.3)	(7.5.5.3)	(oo oo oo oo xo rr)
b	+	+	(7.5.5.3)	(9.7.5.5)	(oo oo oo oo xx rr)
148 a	−	X	(11.0.7.5)	(11.8.7.5)	(oo oo oo oo rr rr)
b	+	X	(11.0.7.5)	(11.9.7.5)	(oo oo oo ox ro rr)
149 a	−	+	(9.9.5.5)	(11.9.7.5)	(oo oo oo xx xo rr)
b	+	+−	(10.9.6.5)	(10.9.6.5)	(xo xo oo xx xx rr)
160 a	+	+	(7.5.5.3)	(7.5.5.3)	(oo oo oo oo xx oo)
b	+	−	(7.5.5.3)	(8.6.5.5)	(oo oo oo oo xx rx)
166 a	−	+	(9.8.5.4)	(10.8.6.5)	(oo oo oo ox oo xx)
b	+	+	(9.8.5.4)	(8.6.5.11)	(oo oo ox ro ox rr)
168 a	+	+	(7.5.5.5)	(9.7.5.5)	(oo oo oo oo xx xx)
b	−	+	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xx xx)
176 a	+	−+	(9.7.5.5)	(11.10.8.5)	(xx xx oo ox xo rr)
b	+	+	(9.0.5.5)	(9. 9.5.5)	(rr oo oo ox xo rr)
189 a	−	+	(7.5.5.4)	(9.0.5.5)	(oo oo oo oo xo xx)
b	+	−	(8.6.5.4)	(11.7.5.5)	(oo oo oo oo xx xx)
191 a	+	−	(9.9.5.4)	(11.10.6.5)	(oo oo oo xx oo rr)
b	+	+	(7.5.5.5)	(9. 7.5.5)	(xx xx oo oo xx rx)
229 a	−	+	(11.0.7.5)	(12.9.7.6)	(xx xx oo ox oo xx)
b	+	+	(11.0.7.5)	(11.0.7.5)	(rr oo oo ox oo rr)
238 a	+	+	(9.9.5.5)	(11.9.7.5)	(xo xo oo xx rr xx)
b	+	−	(11.8.7.5)	(11.9.7.5)	(oo oo oo ox xr rr)
244 a	+	+	(7.5.5.4)	(7.5.5.5)	(oo oo oo oo xx xr)
b	+	−	(7.5.5.5)	(7.5.5.5)	(oo oo oo oo xx rr)
254 a	+	+−	(11.8.7.5)	(11.8.7.5)	(oo oo rx oo rr rr)
b	+	+	(10.8.6.5)	(11.8.7.5)	(oo oo oo oo oo rr)

TABLE 12 (continued)

NUMBER	HAND	CROWN	MAIN LINES		PATTERNS
262 a	+	−	(11.7.5.5)	(11.10.8.5)	(oo oo oo ox xo xo)
b	+	+−	(11.9.7.5)	(11. 9.7.5)	(oo oo oo xx oo rr)
269 a	+	+	(11.9.7.4)	(11.9.7.5)	(oo oo oo xx oo xx)
b	−	X	(11.8.7.4)	(11.9.7.5)	(oo oo oo xx oo xx)
275 a	+	−	(11.0.7.5)	(11.0.7.5)	(oo oo oo or oo rr)
b	−	−	(10.0.6.5)	(11.0.7.5)	(oo oo oo oo oo rr)
276 a	+	−	(11.8.7.5)	(11.0.7.5)	(rr oo ro oo oo xx)
b	+	+	(11.8.7.5)	(11.0.7.5)	(rr oo rr ox rr xx)
296 a	+	+	(11.8.7.5)	(11.8.7.5)	(oo oo oo oo oo xx)
b	−	−	(11.8.7.5)	(11.9.7.5)	(oo oo oo ox oo rx)
302 a	+	+	(9.0.5.1)	(9.7.5.1)	(oo oo oo oo ox xx)
b	−	+	(10.8.6.1)	(8.6.5.4)	(oo oo oo oo ox xx)
303 a	−	+	(9.8.5.4)	(11.8.7.4)	(oo oo oo oo oo xx)
b	+	+	(7.5.5.4)	(7.5.5.4)	(oo oo oo oo xx xx)
305 a	−	+	(10.9.6.5)	(11.9.7.5)	(xr ?o rr xx xx xx)
b	+	+	(9.9.5.5)	(9.9.5.5)	(rr oo rr xx rr rr)
159 x	+	+	(11.8.7.5)	(7.5.5.5)	(oo oo oo oo ox xx)
y	−	+	(9.7.5.3)	(10.0.6.5)	(oo oo oo ox xo rr)
171 x	−	+	(11.9.7.4)	(11.9.7.5)	(oo oo oo xx oo xx)
y	+	+	(11.9.7.4)	(11.9.7.4)	(oo oo oo xx oo xx)
178 x	+	+	(9.7.5.4)	(11.9.7.4)	(oo oo oo ox xo xx)
y	−	+	(10.0.6.4)	(11.9.7.4)	(oo oo oo ox oo xx)
181 x	+	+	(11.9.7.5)	(8.6.5.5)	(oo oo oo xo ox rx)
y	+	−	(7.5.5.1)	(8.6.5.2)	(oo oo oo xx xx rr)
183 x	−	+	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo xx)
y	+	+	(9.7.5.5)	(11.9.7.5)	(oo oo oo rr xr xx)
185 x	+	−	(11.9.7.4)	(11.9.7.5)	(oo oo oo xx oo xo)
y	+	+	(11.9.7.5)	(11.9.7.5)	(xo xo oo xx oo oo)
196 x	+	+	(9.7.5.5)	(9.7.5.5)	(xo xo oo ox xo oo)
y	+	+−	(10.0.5.5)	(9.7.5.5)	(xx xx oo oo ox oo)

TABLE 12 (continued)

NUMBER	HAND	CROWN	MAIN LINES		PATTERNS
211 x	+	−	(9.0.5.3)	(11.9.7.5)	(oo oo oo ox oo rr)
y	+	+	(9.9.5.4)	(11.9.7.5)	(oo oo oo xx oo rr)
233 x	−	+	(7.5.5.5)	(7.9.7.5)	(xx xx oo xx xx rr)
y	+	+	(7.5.5.3)	(10.9.6.5)	(oo oo oo ox xo rr)
279 x	+	+	(11.8.7.4)	(11.9.7.4)	(oo oo oo ox oo xx)
y	+	+−	(11.8.7.4)	(11.8.7.4)	(oo oo oo oo oo xx)
293 x	+	−	(9.7.5.5)	(11.9.7.5)	(xx xx oo ox xr rr)
y	+	+	(11.9.7.5)	(9.9.5.5)	(oo oo oo xx rr xx)
101 a	+	+	(10.9.6.4)	(11.9.7.4)	(oo oo oo xx rr xx)
x	−	+	(10.9.6.4)	(11.9.7.4)	(oo oo oo xx rr xx)
132 a	+	+	(9.7.5.5)	(9.9.5.5)	(oo oo oo ox xx xx)
x	+	−	(11.8.7.5)	(10.7.6.5)	(oo oo oo ox xx xx)
137 a	+	−	(11.7.5.3)	(11.9.7.5)	(oo oo oo ox xo rr)
x	+	+	(10.9.6.5)	(11.9.7.5)	(oo oo oo ox rr rr)
138 a	+	−	(7.5.5.3)	(8.6.5.3)	(oo oo oo oo xx rr)
x	+	+	(7.5.5.3)	(10.9.6.3)	(oo oo oo ox xo rr)
155 a	+	+	(7.5.5.4)	(7.5.5.5)	(oo oo oo oo xx xx)
x	−	+−	(7.5.5.4)	(7.5.5.4)	(oo oo oo oo xx xx)
158 a	+	+	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xr rr)
x	−	+	(9.9.5.1)	(11.9.7.1)	(oo oo oo xx oo rr)
163 a	+	−	(7.5.5.5)	(9.7.5.5)	(ro oo oo oo xx oo)
x	+	+	(7.9.5.5)	(7.5.5.5)	(oo oo oo xo xx rr)
172 a	+	−	(9.7.5.3)	(9.8.5.3)	(oo oo oo oo xo rr)
x	+	−	(9.0.5.5)	(11.0.7.5)	(oo oo oo ox oo rr)
190 a	+	−	(11.0.7.5)	(11.9.7.5)	(xo xo oo ox oo rr)
x	+	+	(11.8.7.5)	(11.9.7.5)	(oo oo oo ox oo rr)
198 a	+	++	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xx rr)
x	−	+	(9.7.5.5)	(11.9.7.5)	(oo oo oo ox xo rr)
207 a	+	+	(11.8.7.5)	(11.9.7.5)	(xo xo xx ox xo rr)
x	+	+−	(11.7.7.5)	(11.9.7.5)	(oo oo oo ox xo rr)
222 a	−	−	(11.9.7.5)	(11.11.9.5)	(xx xx oo xx oo oo)
x	+	+	(11.9.7.5)	(11. 9.7.5)	(oo oo oo xx oo oo)

TABLE 12 (continued)

NUMBER	HAND	CROWN	MAIN LINES		PATTERNS
224 a	+	−	(11.8.7.5)	(11.9.7.5)	(oo oo oo xx oo rr)
x	+	+	(7.8.5.5)	(11.9.7.5)	(oo oo oo xx xx rr)
232 a	+	+	(11.0.7.5)	(11.0.7.5)	(oo oo oo oo oo rr)
x	−	+−	(11.0.7.5)	(11.0.7.5)	(oo oo oo oo oo rr)
246 a	+	−	(9.7.5.5)	(7.5.5.4)	(oo oo oo oo xx rx)
x	+	+	(7.7.5.5)	(11.9.7.5)	(oo oo xx xx xx rr)
272 a	+	+	(11.8.7.5)	(11.9.7.5)	(oo oo oo ox oo rr)
x	+	−	(9.7.5.5)	(11.8.7.5)	(oo oo oo oo xo xr)
287 a	−	+	(11.9.7.1)	(9.9.5.3)	(oo oo oo xx oo rr)
x	+	+	(9.9.5.3)	(10.9.6.5)	(oo oo oo xx oo rx)
102 a	+	+	(9.7.5.4)	(11.9.7.5)	(oo oo oo ox xo xx)
b	+	+	(9.7.5.5)	(7.5.5.5)	(oo oo oo oo ox rr)
150 a	+	+	(9.0.5.5)	(11.0.7.5)	(oo oo oo oo oo rr)
b	+	+	(11.0.7.5)	(11.0.7.5)	(oo oo oo ox oo rr)
162 a	+	+	(9.9.5.5)	(9.9.5.5)	(oo oo oo xx oo xx)
b	+	+	(9.7.5.4)	(9.7.5.5)	(oo oo oo oo xx xx)
179 a	+	+	(8.6.5.4)	(8.6.5.4)	(oo oo oo oo xx xx)
b	+	+	(8.6.5.4)	(8.6.5.4)	(oo oo oo oo xx rx)
180 a	+	+	(7.5.5.3)	(7.5.5.4)	(oo oo oo oo xx rx)
b	+	+	(7.5.5.4)	(7.5.5.4)	(oo oo oo oo xx xr)
214 a	+	+	(9.9.5.5)	(11.9.7.5)	(oo oo oo xx oo xr)
b	+	+	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo xr)
253 a	+	+	(9.9.5.3)	(10.9.7.5)	(oo oo oo xx oo oo)
b	+	+	(9.9.5.5)	(9.9.5.5)	(oo oo oo xx oo oo)
308 a	+	+	(11.0.7.5)	(11.0.7.5)	(oo oo oo oo oo xx)
b	+	+	(11.9.7.5)	(11.9.7.5)	(ro xo xx xx rr rx)
107 x	+	+	(8.6.5.4)	(8.6.5.4)	(oo oo oo oo xx xx)
y	+	+	(7.5.5.4)	(8.6.5.4)	(oo oo oo oo xx xx)
109 x	+	+	(10.0.6.5)	(8.6.5.5)	(xx xx oo oo ox oo)
y	+	+	(7.5.5.5)	(11.0.7.5)	(xx xx oo oo xo xo)
110 x	+	+	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xx xx)
y	+	+	(7.5.5.5)	(7.5.5.5)	(oo oo oo oo xx xx)

TABLE 12 (continued)

NUMBER	HAND	CROWN	MAIN LINES		PATTERNS
129 x	+	+	(11.8.7.5)	(11.9.7.5)	(xx oo oo ox oo rx)
y	+	+	(11.8.7.5)	(11.9.7.5)	(xx oo oo ox oo rx)
147 x	+	+	(9.9.5.4)	(9.7.5.4)	(oo oo oo xo ox xx)
y	+	+	(9.9.5.4)	(9.9.5.4)	(oo oo oo xx oo xx)
156 x	+	+	(11.9.7.4)	(11.9.7.4)	(oo oo oo xx oo xx)
y	+	+	(9.7.5.4)	(9.7.5.4)	(oo oo oo oo xx xx)
177 x	+	+	(7.5.5.3)	(8.6.5.3)	(oo oo oo oo xx rr)
y	+	+	(8.6.5.3)	(8.6.5.5)	(oo oo oo oo xx rr)
183 x	+	+	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo rx)
y	+	+	(9.7.5.5)	(11.9.7.5)	(oo oo oo ox xo xx)
201 x	+	+	(11.9.7.5)	(11.9.7.5)	(oo oo oo xx oo xx)
y	+	+	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xx rr)
218 x	+	+	(9.8.5.3)	(9.8.5.3)	(oo oo oo oo rr oo)
y	+	+	(7.5.5.3)	(7.5.5.3)	(oo oo oo oo xx oo)
233 x	+	+	(7.5.5.3)	(7.9.7.5)	(xx xx oo xx xx oo)
y	+	+	(7.5.5.3)	(10.9.6.5)	(oo oo oo ox xo oo)
274 x	+	+	(11.0.7.5)	(11.0.7.5)	(oo oo oo oo oo xx)
y	+	+	(11.0.7.5)	(11.0.7.5)	(oo oo oo oo oo xx)
301 x	+	+	(9.0.5.5)	(11.0.7.5)	(oo oo oo oo oo rr)
y	+	+	(8.7.10.5)	(11.0.7.5)	(oo oo oo oo xo rr)
304 x	+	+	(7.0.5.4)	(7.5.5.4)	(oo oo oo oo ox rx)
y	+	+	(7.5.5.4)	(11.9.7.5)	(oo oo oo ox xo rx)
306 x	+	+	(9.7.5.5)	(9.7.5.5)	(oo oo oo oo xx rr)
y	+	+	(7.5.5.5)	(11.8.7.5)	(oo oo oo oo xo rr)

MENTAL AND PHYSICAL TRAITS

Younger versus older twins

The argument that older twins show no greater degree of similarity than younger twins, and that, hence, nature is more potent than nurture, was first advanced by GALTON (1883). Since that time other evidence to substantiate his theory has been presented by THORNDIKE (1905) and MERRIMAN (1924). GALTON'S conclusions were based on verbal reports and cannot be objectively stated. THORNDIKE'S coefficients for younger twins (9 to 11 years) averaged 83; for older twins (12-14 years) 70. MERRI-

MAN in his study was able to take much more adequate measurements due to the development of standardized tests. His coefficients for younger twins (5 to 9 years) averaged 77; for older twins (10 to 16 years) 67. The results of my study are given in table 13.

The evidence, though somewhat variable, is, nevertheless, conclusive. Even the averages in each case reveal no greater similarity among the older twins than among the younger twins. THORNDIKE concludes, with reference to his data, that the most probable explanation of differences is chance. MERRIMAN reaches the same conclusion. An inspection of my data shows that even in traits most subject to training there are no large differences. One might expect greater similarities in reading, arithmetic and writing, abilities subject to training, but such similarities do not materialize except in reading.

TABLE 13

Older versus younger twins. About 100 cases in each group.

TRAIT	90 to 156 MONTHS	157 to 238 MONTHS	DIFFERENCE
Intelligence quotients	64	73	+09
Reading quotients	44	57	+13
Arithmetic, accuracy	59	50	−09
Arithmetic, speed	59	57	−02
Memory for digits	36	34	−02
Handwriting, quality	49	58	+09
Handwriting, speed	66	55	−11
Averages	54	55	+01

Like-sex versus unlike-sex twins

Neither THORNDIKE nor GALTON report any studies of the differences in mental traits between like- and unlike-sex pairs of twins. The only adequate data available are those of MERRIMAN (1924, p. 29) which are given in table 14.

TABLE 14

Like- versus unlike-sex twins (MERRIMAN).

TEST	LIKE-SEX	UNLIKE-SEX	DIFFERENCE
Stanford-Binet (intelligence quotients)	.867	.504	.363
Army Beta (intelligence quotients)	.908	.732	.176
National Intelligence Test (intelligence quotients)	.925	.867	.058
Teacher estimates	.654	.266	.388
Averages	.838	.592	.246

MERRIMAN offers his results as evidence favoring the theory of two types of twins, one-egg and two-egg. It seems logical to suppose that the twins derived from a single germ should be more nearly alike than those derived from two separate germs and since the one-egg twins are included in the like-sex group, the higher correlation is attributed to the circumstance of origin. MERRIMAN'S distribution of intelligence-quotient differences points in the same direction.

My own data make it possible to secure three groupings according to sex. It will be seen that my results corroborate those of MERRIMAN. In general intelligence, memory for digits, and speed in handwriting, the differences between the abxy and ax pairs is marked. In reading, an ability much subject to training, there is only a slight difference, while in arithmetic the difference is considerable.

TABLE 15

Like- versus unlike-sex twins. About 70 cases in each group.

TRAITS	AB	XY	AVERAGE	AX	DIFFERENCE
Intelligence quotients	81	73	77	56	+21
Reading quotients	62	56	59	56	+03
Arithmetic, accuracy	72	65	69	35	+34
Arithmetic, speed	70	69	70	39	+31
Addition, accuracy	66	35	51	34	+17
Addition, speed	65	56	61	40	+21
Subtraction, accuracy	65	63	64	44	+20
Subtraction, speed	69	51	60	23	+37
Multiplication, accuracy	48	32	40	09	+31
Multiplication, speed	60	39	50	25	+25
Division, accuracy	07	06	07	09	−02
Division, speed	55	64	60	30	+30
Memory for digits	44	36	40	25	+15
Handwriting, quality	69	68	69	37	+32
Handwriting, speed	82	84	83	37	+46
Averages	61	53	57	33	+24

In general, then, like-sex pairs of twins show greater similarities than unlike-sex pairs. It should be noted, however, that the very circumstance of sex tends to vary environment and the older the twins become the greater the environmental difference. A boy and a girl brought up in the same home are not in the same environment. Almost from birth the environment of the girl has been different from that of the boy, even under the same parental roof. While I see no method of eliminating these factors from my data, they do exist and may have an important bearing on twin resemblances. The fact is well attested by the evidence

that like-sex pairs of twins show a greater degree of intellectual resemblance than unlike-sex pairs of twins, and it is probable that these differences exist by virtue of original nature, since environments which seem to be similar have little influence in modifying the relationships.

Twins versus other sibs

Several studies have been made of sib resemblance, all with essentially the same result. PEARSON'S (1904) data are frequently quoted. His correlation coefficients average for the brother-brother data, 52; for the sister-sister, 61; and for the brother-sister, 52.

Miss EMILY DEXTER (1915) of the UNIVERSITY OF WISCONSIN made a study of sib resemblance based on data collected on approximately 184 brothers and sisters in the UNIVERSITY OF WISCONSIN and on about 69 high-school students. In table 16 correlation coefficients in English, language, mathematics, history and science are given. In the same manuscript Miss DEXTER reports the following correlations in general intelligence, the data used being based on intelligence quotients and coefficients of brightness obtained on the Dearborn Test and the National Intelligence Test given to about 800 children in the elementary schools of Madison, Wisconsin (see table 17).

TABLE 16

Sib resemblance in scholarship (DEXTER).

GROUPS	SCHOLARSHIP AVERAGE	ENGLISH	LANGUAGE	MATHEMATICS	HISTORY	SCIENCE
University						
All pairs	34	28	23	07	29	20
Brother-brother	40	14	20	05	35	31
Sister-sister	34	50	34	03	21	15
Brother-sister	32	02	07	07	26	21
High-school						
All pairs	28	23	09	19	33	35

TABLE 17

Sib resemblance in general intelligence (DEXTER).

GROUPS	GROUP 1	GROUP 2	GROUPS 1+2	GROUP 3
All pairs	53	45	49	61
Brother-brother	55	49	53	66
Sister-sister	42	38	40	52
Brother-sister	54	46	51	63

From an inspection of these studies it is apparent that sib resemblance is approximately 50. It has already been seen from data presented that THORNDIKE places twin resemblance at 80. MERRIMAN places it at the same figure for like-sex pairs, but finds a twin resemblance of about 60 for unlike-sex pairs. The average of all traits in the like-sex twins in my study is approximately 55; while that for unlike-sex twins is approximately 30. In general intelligence and handwriting my figures more nearly approximate the commonly accepted 80 for like-sex pairs and 50 for unlike-sex pairs. But regardless of the lower average figure, the difference in correlation between like- and unlike-sex pairs is still large.

Thus, the evidence all tends in the same general direction. Unlike-sex pairs of twins show a degree of resemblance about equal to that of other sibs, while like-sex pairs show a correlation considerably higher. The degree of resemblance between father and son, based on findings of ELDERTON (1907) and others, may be said to be about 40 and that for cousins, 25. We have, then, a chain of evidence as follows:

Like-sex twins	80
Unlike-sex twins	50
Other sibs	50
Parent-child	40
Cousins	25

The apparent conclusion is that the closer the relationship, the greater the resemblance. Unlike-sex pairs of twins approximate the resemblance of other sibs. This is what is naturally expected if two ova are fertilized by two separate sperm. The twins, to all intents and purposes, bear to each other a fraternal relationship. Then, if all twins are of two-egg origin, the correlation coefficients for like- and unlike-sex pairs should be approximately the same. The rather marked difference, however, which the facts reveal, has been attributed by most investigators to a difference in origin, that is, approximately one-half of all like-sex pairs are of one-egg origin and therefore resemble each other more than the twins of two-egg origin. If the one-egg group of like-sex twins could be separated from the two-egg group, we would probably have in the former case a correlation approximating 90; in the latter case, a correlation approximating 50.

Native versus acquired traits

While environment seems impotent to change the general intellectual resemblance of twins, the evidence on traits much subject to training is

somewhat conflicting. The significant fact is that coefficients for multiplication, and particularly for division, are much lower than for addition and subtraction. It is in addition and subtraction that the twins have had most

TABLE 18

Twin resemblance in the fundamental processes of arithmetic (about 70 cases in each group except in division, where the number of cases is about 50 for each group.)

A. Accuracy

PAIRS	ADDITION	SUBTRACTION	MULTIPLICATION	DIVISION
ab	66	65	48	07
xy	35	63	32	06
ax	34	44	09	09

B. Speed

ab	65	69	60	55
xy	56	51	39	64
ax	40	23	25	30

training, they have had less in multiplication; and in the lower grades, very little in division. In fact, in some schools long division had not been taught when the tests were given. In addition and subtraction the individual's performance has been stabilized by practice. In multiplication and division his performance is still exceedingly variable, and as a consequence measurements of his ability are unreliable. The coefficient of correlation does not express the true relationship. The variability in performance and the consequent difficulty in measuring the true ability probably account for the lower correlations in multiplication and division.

Handwriting is an ability much subject to training. Yet here the effect of training is not at all clear:

Pairs	*Quality*	*Rate*
Younger pairs	49	66
Older pairs	58	55

In speed, training seems to make twins more unlike, while in quality the opposite is the case. The data may not, however, reveal the essential facts. In school, training in handwriting has usually ceased by the time the ninth grade is reached. It seems to be the general situation that the effects of training are rapidly lost. If the degree of resemblance could be determined for successive age groups, from the time that training begins until after it ceases, it seems reasonable to suppose that we would find

similarities increasing with training, probably within limits determined by sex and original nature.

In this connection it is interesting to note the varying degrees of resemblance in handwriting which have been reported, both in the case of twins and of other sibs. GALTON (1883, p. 157) says,

> "Most singularly, the one point in which similarity is rare is handwriting. I cannot account for this, considering how strongly handwriting runs in families, but I am sure of the fact. I have only one case in which nobody, not even the twins themselves, could distinguish their own notes of lectures, etc.; barely two or three in which the handwriting was undistinguishable by others, and only a few in which it was described as closely alike. On the other hand, I have many in which it is stated to be unlike, and some in which it is alluded to as the only point of difference. It would appear that the handwriting is a very delicate test of difference in organization—a conclusion which I commend to the notice of enthusiasts in the art of discovering character by the handwriting."

In contrast to this conclusion, my own results are quite revealing. The data upon which these correlations were computed were secured from the handwriting of 200 pairs of twins measured by the Kansas City Handwriting Scale. Each specimen was scored by three competent judges,

TABLE 19

Resemblance in the handwriting of twins.

GROUP	QUALITY	SPEED
ab	69	82
xy	68	84
ax	37	37
Younger	49	66
Older	58	55

twice by judge A, and once each by judges B and C. The reliability coefficients of the judgments vary from 81 to 92, showing a rather high consistency in the four judgments (KRAMER 1924). It is safe to say from this study that the degree of resemblance in the quality of the handwriting of twins as measured by the Kansas City Scale is, for like-sex pairs, 70; for unlike-sex pairs, 40. In speed it is, for like-sex pairs, 80; for unlike-sex pairs, 40.

It should be noted, however, that quality alone, as measured by a scale, does not determine similarity. This is well illustrated by plate 4. These specimens receive average scores of 10.00 and 10.25 on the Kansas City Scale (four expert judges) and yet there would not be the slightest danger

HANDWRITING

These two specimens of the handwriting of a pair of twins were scored 10.25 and 10.00 by four judges on the Kansas City Handwriting Scale. While apparently very similar in quality they are markedly different in appearance.

SCORE: Rate. 8.3...Quality. 10.25 No. 220-a

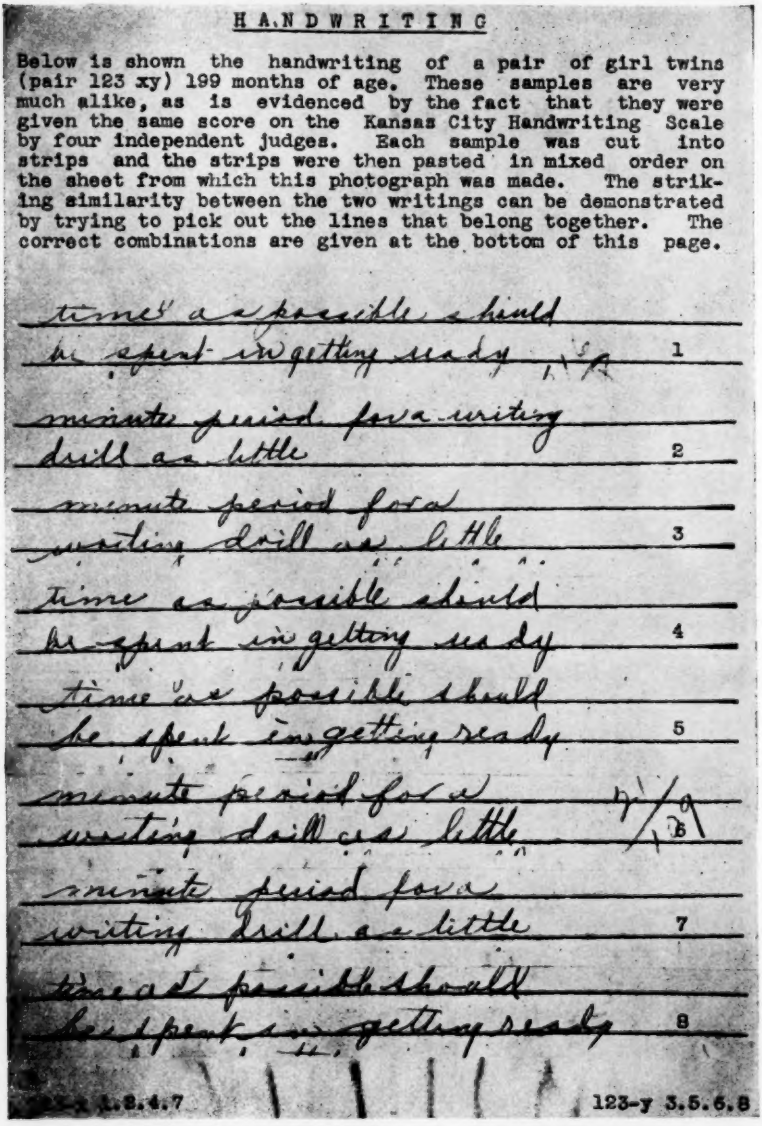
If there is a ten minute period for a writing drill as little time as possible should be spent in getting ready and in putting away material. If there is a ten minute period for a little writing drill as little

SCORE: Rate 11.5...Quality. 10.00 No. 220-X

If there is a ten minute period for a writting drill as little time as possible should be spent in getting ready and in putting away material. If there is a ten minute period for a writting drill as little time as possible should be spent in getting ready and in putting away material

HANDWRITING

Below is shown the handwriting of a pair of girl twins (pair 123 xy) 199 months of age. These samples are very much alike, as is evidenced by the fact that they were given the same score on the Kansas City Handwriting Scale by four independent judges. Each sample was cut into strips and the strips were then pasted in mixed order on the sheet from which this photograph was made. The striking similarity between the two writings can be demonstrated by trying to pick out the lines that belong together. The correct combinations are given at the bottom of this page.


time as possible should
be spent in getting ready 1
minute period for a writing
drill as little 2
minute period for a
writing drill as little 3
time as possible should
be spent in getting ready 4
time as possible should
be spent in getting ready 5
minute period for a
writing drill as little 6
minute period for a
writing drill as little 7
time as possible should
be spent in getting ready 8
123-x 1.2.4.7
123-y 3.5.6.8

of mistaking one for the other. On the other hand the specimens of plate 5 are so nearly alike that a careful study of the peculiarities of letters is necessary before one specimen can be distinguished from the other. Similarity in appearance is largely determined by such obvious characteristics as size and shape of letters, boldness of stroke, and slant, and not by the more subtle characteristics of "quality." GALTON's conclusion, based on the test he applied, is probably correct. On the other hand the degree of resemblance, measured in terms of quality and speed, is much higher than his conclusions might lead one to believe.

PEARSON (1904) found resemblance in handwriting of sibs to be 52. STARCH (1917) has reported two studies with widely varying results:

	1915	*1917*
Quality	06	46
Speed	18	72

The 1915 study was based on 24 pairs of sibs; the 1917 study, on 18 pairs. One fact in STARCH's results and my own may be pointed out, namely, that if unlike-sex twins represent a fraternal relationship, then STARCH's coefficients of correlation in the 1917 study and my own are in practical agreement as far as quality is concerned. But in speed, STARCH's coefficient exceeds the usual coefficient of sib resemblance.

Data	*Quality*	*Speed*
STARCH (single-birth sibs)	46	72
LAUTERBACH (unlike-sex twins)	37	37

In memory for digits the evidence is clear; but in intelligence quotient and reading quotient the older twins show a slightly closer resemblance than the younger. A summary of the evidence would seem to indicate that training has very little effect either upon native or acquired traits.

TABLE 20

Resemblance in general intelligence, reading and memory for digits.

GROUP	INTELLIGENCE QUOTIENT	READING QUOTIENT	DIGITS
Younger pairs.....	64	44	36
Older pairs.....	73	57	34

The intellectual level of a twin population

The intellectual level of a twin population was first investigated by MERRIMAN (1924), who made a comparison (table 21) of the intelligence quotients of about 200 pairs of twins with the intelligence quotients of

TABLE 21

The average intelligence quotients of various groups of twins (MERRIMAN).

GROUP	FREQUENCY	AVERAGE INTELLIGENCE QUOTIENT
All twin pairs	105	96
Pairs 5 to 9 years old	47	99
Pairs 10 to 16 years old	58	94
Like-sex pairs	67	97
Like-sex pairs 5 to 9 years old	29	99
Like-sex pairs 10 to 16 years old	38	95
Unlike-sex pairs	38	95
Unlike-sex pairs 5 to 9 years old	18	98
Unlike-sex pairs 10 to 16 years old	20	92
Girl-girl pairs	40	94
Girl-girl pairs 5 to 9 years old	19	99
Girl-girl pairs 10 to 16 years old	21	90
Boy-boy pairs	27	100
Boy-boy pairs 5 to 9 years old	10	99
Boy-boy pairs 10 to 16 years old	17	101
Boys of unlike-sex pairs	38	95
Girls of unlike-sex pairs	38	95

905 unselected children reported by TERMAN (1916). There are no significant differences between my own results (shown in table 22) and those of MERRIMAN. My age range is from 90 months to 238 months and all ages

TABLE 22

The average intelligence quotients of various groups of twins

GROUP	FREQUENCY	AVERAGE INTELLIGENCE QUOTIENT
Boy-boy pairs	70	94
Girl-girl pairs	75	94
Boy-girl pairs	63	97
Younger pairs	108	98
Older pairs	98	93
Like-sex pairs showing symmetry reversal	36	95
Unlike-sex pairs showing symmetry reversal	27	99
Boy-boy pairs, symmetry reversal pairs omitted	48	94
Girl-girl pairs, symmetry reversal pairs omitted	61	95
Unlike-sex pairs, symmetry reversal pairs omitted	34	95

have been included in the calculations. MERRIMAN kept his groups within the range of 5 to 14 years to compare with the TERMAN data on unselected children. The data are therefore perhaps not quite comparable. But the older twins should have had the advantage in the TERMAN group test and their scores probably run somewhat high. At least they do not overemphasize the facts in the direction of low intelligence. The two sets of averages are quite consistent.

MERRIMAN concluded that a twin population suffers no intellectual handicap. To further test his data, he made a frequency distribution of the intelligence quotients of his 200 pairs of twins in comparison with a similar distribution of the intelligence quotients of TERMAN'S 905 unselected children. In figure 3 all three groups of data are plotted. In spite of the fact that the average intelligence quotient in each case closely approximates the average of the unselected group of children, it will be seen that a considerable percentage of the twins falls below the average of the unselected group.

However, a most striking situation is revealed when my group of twins is distributed on an age-grade chart. The startling fact develops that 45.8 percent of all twins are retarded; 45.6 percent are normal and 8.6 percent are accelerated. Of the boys, 47.9 percent are retarded, 44.4 percent are normal and 7.7 percent accelerated. Of the girls, 43.8 percent are retarded, 46.7 percent are normal, and 9.8 percent are accelerated. The percentages are summarized for convenience in table 23.

TABLE 23

Age-grade distribution of 203 pairs of twins.

	BOYS		GIRLS		TOTALS	
	Number	Percent	Number	Percent	Number	Percent
Normal	87	44.4	98	46.7	185	45.6
Retarded	94	47.9	92	43.8	186	45.8
Accelerated	15	7.7	20	9.5	35	8.6
Totals	196	100.0	210	100.0	406	100.0

In the case of twins we actually have more retardates than normal pupils! Is this retardation to be attributed to a lower general intelligence level in the twin population?

An investigation of over-age children was made by the STATE DEPARTMENT OF EDUCATION in Wisconsin (RANKIN 1916) for the years 1913-14. The average percentage of retardates reported is 56.3; of accelerates, 12.2; of normal pupils, 31.5.

In progress in school the twins are on a par with the school population of which they are a part. There is no evidence, therefore, which warrants the assumption that the intellectual level of a twin population is lower than that of the population in general.

Characteristics of symmetry-reversal groups

It is of interest to note the resemblance, both mental and physical, of the group of twins which manifest symmetry reversal in handedness and

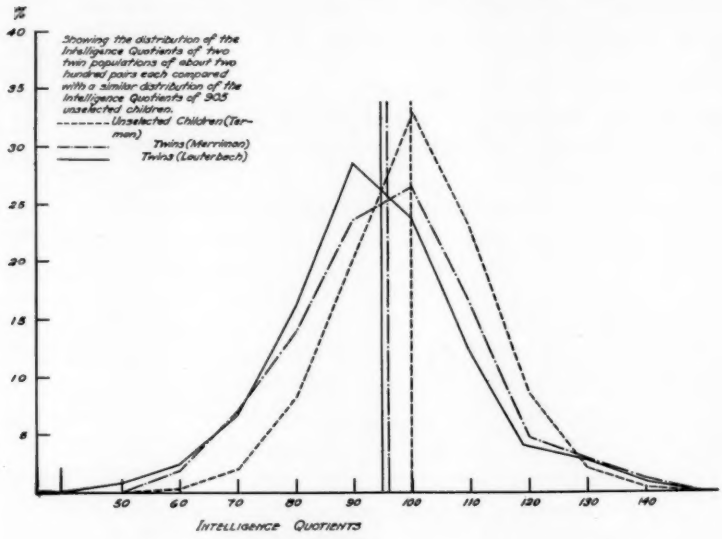


FIGURE 3

whorl of the head-hair. These resemblances are shown in table 24. Theoretically, if symmetry reversal is an indication of the one-egg origin of twins, these groups ought to be more nearly alike than any others. But the data reveal almost the opposite case. In physical traits this disparity is most striking.

Here the average of the coefficients drops from .77 for the abxy group to .59, when only the members of the abxy group which show symmetry reversal are taken. If there are two types of twins, similarity or dissimilarity seems to offer no clue for the identification of either group and symmetry reversal certainly adds nothing to clarify the situation.

TABLE 24

Coefficients of correlation in traits of the symmetry-reversal (SR) groups as compared with the abxy and the ax groups.*

TRAIT	ABXY	ABXYSR	AX	AXSR
Intelligence quotients	.77	.77	.56	.59
Reading quotients	.59	.65	.56	.69
Arithmetic, accuracy	.69	.61	.35	.19
Arithmetic, speed	.70	.73	.39	.25
Memory for digits	.40	.31	.25	.49
Handwriting, quality	.69	.65	.37	.41
Handwriting, speed	.83	.82	.37	.31
Averages	.67	.65	.41	.42
Cephalic index	.67	.73	.59	.49
Weight	.89	.65	.50	.53
Height, standing	.80	.54	.53	.44
Height, sitting	.73	.43	.59	.55
Averages	.77	.59	.55	.50

* SR stands for symmetry reversal. AbxySR means the group of like-sex twins showing symmetry reversal; axSR means the group of unlike-sex twins showing symmetry reversal.

Physical traits

THORNDIKE (1905) reports coefficients of correlation in physical traits of 31 pairs of twins which vary from 65 for finger-joint length to 83 for height sitting. He attacked the problem of two types of twins by figuring correlation coefficients for single pairs and then making a frequency distribution of these coefficients. The distribution shows a unimodal curve skewed toward the higher end of the scale.

TABLE 25

Resemblance in physical traits shown by coefficients of correlation

TRAIT	AB	XY	AX	YOUNGER	OLDER
Height, standing	.72	.87	.53	.61	.65
Height, sitting	.70	.76	.59	.60	.58
Weight	.93	.85	.50	.59	.64
Cephalic index	.63	.71	.59	.72	.61
Averages	.75	.80	.55	.63	.62

Correlations computed by myself on data collected on 200 pairs of twins are recorded in table 25. A study of the table reveals at once the striking difference in degree of resemblance between like-sex pairs and

TABLE 26

Summary table of correlation coefficients and probable errors. Age held constant.

TRAIT	AB	XY	AX	ABXYSR	AXSR	YOUNGER	OLDER
Intelligence quotients	.81 ± .03	.73 ± .04	.56 ± .06	.77 ± .05	.59 ± .06	.64 ± .04	.73 ± .03
Reading quotients	.62 ± .05	.56 ± .05	.56 ± .06	.65 ± .06	.69 ± .07	.44 ± .05	.57 ± .05
Arithmetic, accuracy	.72 ± .06	.65 ± .07	.35 ± .08	.61 ± .07	.19 ± .13	.59 ± .04	.50 ± .05
Arithmetic, speed	.70 ± .06	.69 ± .06	.39 ± .07	.73 ± .06	.25 ± .12	.59 ± .04	.57 ± .05
Addition, accuracy	.66 ± .05	.35 ± .07	.34 ± .08	.....	.....	.....	.....
Addition, speed	.65 ± .05	.56 ± .06	.40 ± .07	.....	.....	.....	.....
Subtraction, accuracy	.65 ± .05	.63 ± .05	.44 ± .07	.....	.....	.....	.....
Subtraction, speed	.69 ± .04	.51 ± .06	.23 ± .08	.....	.....	.....	.....
Multiplication, accuracy	.48 ± .06	.32 ± .07	.09 ± .09	.....	.....	.....	.....
Multiplication, speed	.60 ± .05	.39 ± .07	.25 ± .08	.....	.....	.....	.....
Division, accuracy	.07 ± .09	.06 ± .05	.09 ± .09	.....	.....	.....	.....
Division, speed	.55 ± .06	.64 ± .02	.30 ± .09	.....	.....	.....	.....
Memory for digits	.44 ± .07	.36 ± .07	.25 ± .08	.31 ± .10	.49 ± .09	.36 ± .06	.34 ± .06
Handwriting, quality	.69 ± .04	.68 ± .04	.37 ± .08	.65 ± .07	.41 ± .10	.49 ± .05	.58 ± .05
Handwriting, speed	.82 ± .03	.84 ± .02	.37 ± .08	.82 ± .04	.31 ± .11	.66 ± .04	.55 ± .05
Height, standing	.72 ± .06	.87 ± .03	.53 ± .07	.54 ± .08	.44 ± .10	.61 ± .04	.65 ± .04
Height, sitting	.70 ± .06	.76 ± .05	.59 ± .06	.43 ± .09	.55 ± .09	.60 ± .05	.58 ± .05
Weight	.93 ± .02	.85 ± .03	.50 ± .07	.65 ± .07	.53 ± .09	.59 ± .05	.64 ± .04
Cephalic index	.63 ± .05	.71 ± .04	.59 ± .06	.73 ± .05	.49 ± .09	.72 ± .03	.61 ± .05

unlike-sex pairs. The difference is most marked in weight and least marked in cephalic index. It is probable, however, that these differences can be attributed to sex.

Maturity seems to have no influence on the degree of resemblance among twins, since the data on the older twins yield approximately the same coefficients of resemblance as data on the younger twins.

CONCLUSIONS

1. Older twins show no greater degree of resemblance than younger twins. This is in conformity with the findings of THORNDIKE (1905) and MERRIMAN (1924), and favors the argument that heredity is more potent than environment.

2. Like-sex pairs of twins show a greater degree of resemblance than unlike-sex pairs. These differences in degree of similarity are attributed by MERRIMAN to the circumstance of origin (monozygotic or dizygotic). The facts seem to favor the theory.

3. Twins show a greater degree of resemblance than other sibs. It has also been shown that single-birth sibs are more nearly alike than parents and children; and parents and children, than cousins. The inference follows that the closer the relationship, the greater the resemblance.

4. Unlike-sex pairs of twins show a degree of resemblance about equal to that of single sibs. A fraternal relationship is thus indicated.

5. There seems to be no definite tendency among twins toward greater similarity in acquired traits than in native ability. The evidence is somewhat conflicting, a fact noted by THORNDIKE.

6. There is no evidence which warrants the assumption that twins are intellectually handicapped. MERRIMAN also presents data which seem to favor a normal intellectual level in the twin population.

7. About twenty percent of all twin pairs show symmetry reversal in handedness.

8. About twenty-five percent of all twin pairs show symmetry reversal in whorl of the head-hair.

9. About thirty-five percent of all twin pairs show symmetry reversal in handedness or whorl of the head-hair or both.

10. Symmetry reversal cannot be accepted as evidence of the monozygotic origin of twins, for the reason that unlike-sex pairs as well as like-sex pairs manifest the phenomenon. NEWMAN and WILDER advance the theory that symmetry reversal is an evidence of the monozygotic origin of human twins. The facts will not substantiate the theory unless the possibility is admitted that monozygotic twins may be of unlike sex.

11. Left-handedness is closely associated with twinning. This is evidenced by the large number of twins who are left-handed, by a study of the genealogies of twin-bearing families, and by the circumstance of "situs inversus viscerum "among both twins and left-handed individuals.

12. It may be that left-handedness and twinning are the result of identical or similar causes. This inference rests on the apparent intimate connection betweem left-handedness and twinning.

13. Palm patterns afford no certain means of identifying monozygotic twins. Unlike-sex pairs of twins may show identity of palm patterns and reveal symmetry reversal.

For the sake of completeness there may be added certain conclusions deduced from other evidence.

14. The monozygotic origin of quadruplets among armadillos has been established by NEWMAN. By analogy, twins among other vertebrates, including man, may have a similar genesis.

15. The dissection of conjoined twins, and X-ray examinations of their anatomy, favors the theory of the monozygotic origin of twins by fission in the fertilized ovum.

16. An examination of the foetal membranes of twins at birth has frequently revealed a single placenta and a single chorion. Biologists

maintain that such a condition is the result of genesis from a single ovum.

17. Sex ratios among twins favor the theory of two types of twins the actual ratio being approximately 1 : 1 : 1, whereas, if there were only one type, it ought, by the law of chance, to be approximately 1 : 2 : 1.

18. MERRIMAN has shown statistically that a distribution of the intelligence quotients of a twin population represents two types of population and he concludes that these two types are determined by one-egg and two-egg genesis.

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THE RESEMBLANCE BETWEEN TWINS, A STATISTICAL EXAMINATION OF LAUTERBACH'S MEASUREMENTS

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INTRODUCTORY

In 1919 the author called attention (FISHER 1919) to the remarkable conclusions which appeared to flow from the measurements of twins obtained by THORNDIKE (1905) from the New York schools. At that time this was the only considerable body of measurements available, and although physical measurements were given for only 39 pairs, of which 8 were of unlike sex, the discrepancy between the results and those of the accepted biological theory was so sharp that its statistical significance was not in doubt. The main points of discrepancy were as follows:

(a) The twins of unlike sex showed an average correlation of 0.78, a value much above the value 0.50 to be expected from children related fraternally; since the average of all twins was 0.85, it appeared that twins of unlike sex were not appreciably less alike than twins of like sex. This fact, if it stood alone, would merit little statistical weight, since only eight pairs of unlike sex were available.

(b) The degree of resemblance between each pair in each particular measurement agreed in its curve of distribution remarkably closely with the curve to be expected theoretically from homogeneous material. If some twins differed from others in their closeness of genetic kinship, it was to be expected that this heterogeneity should make the group of values more variable than it was actually found to be.

(c) Twins chosen as especially alike in one trait were found, when other traits were compared, to show no more than the average degree of resem-

blance. THORNDIKE had not failed to remark this surprising fact, which he described by the term "specialization of resemblance." The correlation between the measure of resemblance of the same pair of twins in different traits, was found in THORNDIKE's material to be -0.016 with a probable error of only ± 0.028, suggesting that it was in fact zero, and not distinctly positive as was to be expected.

It appeared at the time that there was no alternative but to accept the facts as THORNDIKE had found them, and to attempt to modify the accepted theory. The valuable and extensive data obtained by Professor LAUTERBACH (see foregoing article) seem to render any such modification unnecessary, and to provide for the first time a quantitative demonstration of the different degrees of resemblance between twins of different physiological origin.

It is not indeed possible from an examination of the measurements to divide a group of twins into two distinct classes as "fraternal" and "identical," and so long as this is the case it were perhaps premature to say that all is plain sailing with the theory of twins. The main difficulties, however, raised by THORNDIKE's data are replaced in LAUTERBACH's much more extensive series of measurements by positive confirmation of the accepted theory of uniovular and biovular twins.

CORRELATION BETWEEN TWINS OF UNLIKE SEX

LAUTERBACH's data are sufficiently extensive to determine the correlation between twins of unlike sex with some accuracy. Of the 63 cases, 53 are complete for the four traits, stature, stem length, weight and cephalic index. The great difficulty is that all the pairs are of different ages, and that for the first three traits the growth over the age interval concerned, 7.5 to 19 years, is far from uniform. All three traits show a well marked maximum growth rate, the age of most rapid growth being about 2 years earlier in girls than in boys. The changing growth rate renders the partial correlation eliminating age almost meaningless. A procedure which gets over this difficulty is to fit cubic regression formulae, respectively, to the whole group of boy twins and to the whole group of girls. The deviations from such regression formulae may, as I have shown elsewhere (FISHER 1924), be treated as homogeneous deviates in order to obtain a valid estimate of the correlation. It is still possible that the correlation for twins of mixed sex will be less than that of fraternal twins of the same sex, for factors affecting early or late maturity will inevitably, during the growing period, act less similarly upon twins of unlike sex than on those of like sex; nevertheless, the procedure should be adequate to give a

definite answer to the question whether twins of unlike sex are or are not more alike than ordinary brothers and sisters are known to be.

The sums of squares and sums of products of these deviations are shown in table 1.

TABLE 1

Correlation in twins of unlike sex.

	SUM OF SQUARES		SUM OF PRODUCTS	CORRELATION COEFFICIENT	NUMBER OF CASES
	Boys	Girls			
Stature (mm).....	329,947	358,500	156,441	.4549	63
Stem length (mm)..	50,204	84,206	29.979	.4611	53
Weight (lb).....	14,527	13,813	5,386	.3802	62
Cephalic index.....	.....	.....	.....	.5370	63

The cephalic index shows no age or sex differentiation; the mean value was 806.47 and the variance 1339, the correlation for the boy-girl twins being that given in table 1.

It is apparent that the values agree well with the value to be expected if twins of unlike sex are related in the same manner as ordinary brothers and sisters; the average correlation, 0.4583, with a standard error about ± 0.053, agrees sufficiently well with the usual values, about 0.50, even if we make no allowance for the possibility that the correlation in weight is not really so high as are the correlations in the skeletal measurements.

The contrast with THORNDIKE'S data is not due to difference in treatment. If we take out individual measures of resemblance as was done for THORNDIKE'S data, we obtain the median values for stature 0.585, for stem length 0.405, for weight 0.474, and for cephalic index 0.454, the average being 0.480 and the median of all 241 values being 0.500. These latter estimates are not so accurate as those obtained above, since they depend only on the ratios of the deviations, and ignore their actual values; they simply demonstrate that the two methods yield concordant results. We thus have in these data the first experimental verification of the belief that twins of unlike sex show the same degree of resemblance as do ordinary brothers and sisters.

AVERAGE CORRELATION BETWEEN TWINS OF LIKE SEX

For twins of like sex both measurements will be referred to the same standard, representing the mean measurement for that age in the sex concerned; we may, therefore, use HARRIS'S (1909) abbreviated method of calculation of intraclass correlations. We take the difference in the measurements for each pair of twins, and find the mean square of these

differences; dividing this by the mean variance at fixed age, we have $2(1-r)$, where r is a trustworthy estimate of the correlation. In these intraclass correlations the effect of age is only involved in the estimates of the mean variance at fixed age.

TABLE 2

The mean square differences between twins of like sex.

	STATURE IN MILLIMETERS	STEM LENGTH IN MILLIMETERS	WEIGHT IN FOUR-OUNCE UNITS	CEPHALIC INDEX
Boys	3316	1492	2261	904
Girls	2355	863	1358	542
Together	2826	1180	1800	720

TABLE 3

The mean variances at fixed age in twins of like sex.

	STATURE IN MILLIMETERS	STEM LENGTH IN MILLIMETERS	WEIGHT IN FOUR-OUNCE UNITS	CEPHALIC INDEX
Boys	6068	1314	3134	1313
Girls	4631	1463	3644	1365
Together	5339	1388	3393	1339

TABLE 4

Correlations in twins of like sex, derived from the data of tables 2 and 3.

	STATURE	STEM LENGTH	WEIGHT	CEPHALIC INDEX
Boys	.7268	.4323	.6393	.6558
Girls	.7457	.6891	.8137	.8015
Together	.7353	.5749	.7347	.7310

For stature, weight and cephalic index the correlations, 0.73 to 0.74, are very substantially higher than for twins of unlike sex; for stem length the values, especially that for boys, show no such considerable difference. In this connection it should be mentioned that if the like-sex twins are of two kinds, showing, respectively, "fraternal" and "identical" degrees of resemblance, the mean square differences will be dominated by the former group and the random-sampling errors will be very considerably greater than with homogeneous material.

It is thus possible to ascribe the lower values for stem length to a few exceptionally large unlike deviations among fraternal twins of like sex.

On the other hand, it is definitely impossible to regard the like-sex twins as homogeneous in respect of degree of resemblance with the twins of unlike sex; for in this case the correlations for like-sex twins would not differ from those of twins of unlike sex by more than the random-sampling errors to be expected from homogeneous material. These errors have been studied in detail; the standard error of the correlation coefficient as ordinarily quoted does not provide a reliable test, but, as I have explained elsewhere (FISHER 1925), an accurate test is possible by means of the related quantity, z, which may be regarded as a transformal correlation.

For stature the values of z are compared in table 5.

TABLE 5

Values of z for statures of like- and unlike-sex twins.

	r	z	RANDOM-SAMPLING VARIANCE
Like-sex	.1353	.9402	.006969
Unlike-sex	.4549	.4909	.016667
Difference		+.4493	.023636

The difference in z is 0.4493 with a standard error ± 0.1537. Treating the other values similarly we have the results shown in table 6.

TABLE 6

Differences of like- and unlike-sex twins with respect to the quantity, z.

	STATURE	STEM LENGTH	WEIGHT	CEPHALIC INDEX
Difference in z	+.45	+.16	+.54	+.33
Standard error	±.15	±.17	±.15	±.15

All save stem length show significant differences, and in stem length the difference, though not significant is in the same direction as the others. It is thus obvious that the like-sex twins do not form material homogeneous with those of unlike-sex, but that some or all of them are much more highly correlated. The correlations from LAUTERBACH'S data are considerably lower than those from THORNDIKE'S data ($r = 0.80$), even when we include in the latter one case in five of unlike sex. This suggests that THORNDIKE encountered a considerably higher proportion of identical twins, in addition to a group of twins of unlike sex with unusually close resemblance.

HETEROGENEITY OF TWINS OF LIKE SEX

In view of THORNDIKE'S data which showed no heterogeneity among twins of like sex, it is important to determine if these data show heterogeneity. The most direct test depends on the differences in the measurements of like-sex twins. If d is the difference of any one pair, found by subtracting the less measurement from the greater, and $\bar{d}$ stand for the mean difference, d^2 for the mean of the squared difference, then for a large sample of normally distributed values we should have

$$\overline{d^2} = \frac{\pi}{2}\bar{d}^2$$

whereas, for a mixture of two such populations, with different mean differences, $\overline{d^2} - \frac{\pi}{2}\bar{d}^2$ should be positive. To utilize this fact it is necessary to know the standard error of $\overline{d^2} - \frac{\pi}{2}\bar{d}^2$ and this is found to be

$$\frac{\overline{d^2}}{\sqrt{n}}(2\pi - 6) = \frac{\bar{d}^2}{\sqrt{n}} \times .5321$$

Applying this test to LAUTERBACH'S data, I find the values given in table 7.

TABLE 7

Tests for heterogeneity in like-sex twins.

	STATURE IN MILLIMETERS		STEM LENGTH IN MILLIMETERS		WEIGHT IN FOUR-OUNCE UNITS		CEPHALIC INDEX PER MILLE	
	Boys	Girls	Boys	Girls	Boys	Girls	Boys	Girls
n	71	74	66	65	70	73	68	70
$\bar{d}$	40.479	34.622	26.273	17.923	33.286	26.260	22.544	17.410
$\bar{d}^2$	3316	2355	1492	863	2261	1358	904	542
$\overline{d^2} - \frac{\pi}{2}\bar{d}^2$	+742	+472	+408	+359	+521	+274	+106	+66
S.E.	±209	±146	±98	±57	±144	±85	±58	±34

In all cases there appears to be significant evidence of heterogeneity; in the case of cephalic index the separate values for boys and girls are scarcely significant, but taking boys and girls together they provide significant evidence.

Is this apparent heterogeneity due to heterogeneity of origin? At first sight other causes cannot be excluded. The data are admittedly hetero-

geneous in respect of age, and the fact that we are using deviations from fitted regression curves on age will doubtless introduce some further heterogeneity. The effect ascribable to these two causes may perhaps best be estimated by treating the twins of unlike sex in the same manner. For these the results are given in table 8.

TABLE 8

Tests for heterogeneity in unlike-sex twins.

	STATURE IN MILLIMETERS	STEM LENGTH IN MILLIMETERS	WEIGHT IN FOUR-OUNCE UNITS	CEPHALIC INDEX PER MILLE
n	63	53	62	63
$\bar{d}_2$	60.048	30.434	48.852	30.937
$\bar{d}^2$	5961	1406	4462	1348
$\bar{d}^2-\frac{\pi}{2}\bar{d}^2$	297	−49	713	−155
S.E.	±400	±103	±301	±90

Two of the deviations are positive and two negative; only that for weight is significant, and this is just the trait in which the effect of age heterogeneity should be most marked. The evidence speaks decisively in favor of the view that twins of like sex are heterogeneous in their mode of origin, while those of unlike sex are apparently homogeneous.

On the theory of fraternal and identical twins about 40 percent of those of like sex should be identical. We cannot assume this ratio *a priori* for the particular sample measured by LAUTERBACH. The correlations indicate, for example, that a larger proportion of the girl twins are identical than of the boys.

The proportion identical in the whole group of boys and girls, must be nearly the same for all measurements, and would be absolutely the same if all cases had been completely measured; if we assume that the standard difference is the same for fraternal twins of like sex as it is for twins of unlike sex we may use the figures for cephalic index to estimate the proportion of identical twins present. If a is the standard difference for identical twins, and p the proportion identical, we shall have

$$pa+(1-p)36.715 = 24.997$$
$$pa^2+(1-p)1348 = 720.38$$

whence,

$$a = 16.856$$
$$p = .59007$$

If we adopt the value 59 percent identical, we may infer the correlation in the identical group from the actual correlations of the like-sex pairs,

taking the average value for the unlike-sex pairs, 0.4583, to represent the fraternal correlation; in this way we obtain

	Stature	*Stem length*	*Weight*	*Cephalic index*
Correlation for identical twins	.9278	.6898	.9268	.9205

Apart from stem length the agreement is excellent.

The values obtained for the estimated correlation between identical twins are of great interest, since, if they could be determined with certainty, they would afford a direct measure of the importance of genetic factors in determining these traits. From an examination of PEARSON'S data for the correlation of related adults the author concluded (FISHER 1918) that, if heredity is due to a number of cumulative Mendelian factors, more than 90 percent of the variance must be due to genetic causes. PEARSON'S data referred to stature, span and cubit, and LAUTERBACH'S data not only confirm the fact for stature, but make it probable that it should be extended to cephalic index, and, for children at least, to weight. It should be remembered that the differences observed in these identical twins are absolutely small. The standard difference in stature is only 26 mm, and from my own experience of measuring children a standard error of measurement of 3 to 5 mm would not seem excessive. The effect of random errors of measurement will be to lower the correlations and will be especially important for stem length, when the measurement errors are at least as great as for stature, while the absolute differences are much less. For cephalic index the standard difference is only 17 parts per mille, and an error of 1 mm in head breadth will produce an error of nearly 6 parts per mille. The average of the four correlations as estimated for identical twins, 0.894, will therefore have been subjected to a dilution of uncertain amount due to errors of measurement.

SPECIALIZATION OF RESEMBLANCE

THORNDIKE'S data clearly indicated that twins more alike in one character were not, on the whole, more alike in other characters. This conclusion is so contrary to the accepted hypothesis that, if it were substantiated, that hypothesis must be abandoned.

In the present data three of the characters, height, stem length and weight, are somewhat closely associated together, and the best test of specialization will be to compare resemblance in stature and cephalic index.

The like-sex pairs were divided according as the difference in stature was 0 to 52 mm, or 53 mm upwards, and also according as the difference in cephalic index was 0 to 25, or 26 upwards. The results are given in table 9.

TABLE 9

Boys

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	33	10	43
High.....	20	5	25
Total....	53	15	68

Girls

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	40	11	51
High.....	13	6	19
Total....	53	17	70

Neither table, nor the two thrown together, gives any indication that those more alike in stature are more alike in cephalic index, or *vice versa*. To test the matter more exactly, the mean square difference in stature and cephalic index was found for each class (table 10).

TABLE 10

Mean square difference in stature.

Boys

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	598	13165	3521
High.....	869	11911	3077
Total....	700	12747	3358

Girls

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	444	9634	2426
High.....	899	6218	2578
Total....	555	8428	2467

With boys, those differing greatly in cephalic index have on the average a somewhat less difference in stature, than those with similar cephalic indices; with girls, the reverse is true, but to a less extent. If, however, we confine attention to those with low differences in stature, so excluding the high values which tend to dominate the averages, both sexes show a distinctly lower difference in stature, for the children with similar cephalic indices. Putting the two sexes together we have

	Cases	*Mean square*
Like in cephalic index.....	73	516
Unlike in cephalic index.....	33	881

This difference is just over the verge of significance; by my z test (FISHER 1925, chapter VII) I find $z=0.267$, while the value 0.234 is exceeded by chance in only 5 percent of cases.

Repeating the test for differences in cephalic index, we have the grouping shown in table 11. Again, in the totals, the boys alike in stature show actually greater divergence in the cephalic index, while the girls show the

TABLE 11

Mean square difference in cephalic index.

Boys

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	156	203	167
High.....	2382	1296	2173
Total....	1000	568	904

Girls

Difference in cephalic index	Difference in stature: Low	High	Total
Low.....	122	227	145
High.....	1494	1853	1607
Total....	458	801	542

reverse to a less extent. Confining the comparison to those alike in cephalic index, the two sexes agree, and give

	Cases	*Mean square*
Like in stature.....	73	137
Unlike in stature.....	21	216

By the z test, $z=0.228$, and the 5 percent point is at 0.266.

Both results, therefore, are on the verge of significance, and together seem to establish that, if we exclude the cases of wide discrepancy, twins much alike in head form tend to be more alike in stature, and *vice versa*.

CONCLUSIONS

LAUTERBACH'S physical measurements of about 200 pairs of twins appear to provide unequivocal evidence for the following conclusions:

(1) Twins of unlike sex resemble each other to approximately the same extent as do ordinary brothers and sisters.

(2) Twins of like sex show on the average a considerably closer resemblance.

(3) Twins of like sex are heterogeneous, and are therefore divisible in respect of resemblance into at least two classes.

(4) The data may be interpreted as due to a mixture of identical and fraternal twins, of which about 59 percent appear to be identical. The correlations between identical twins must, on this supposition, be about 0.9 or over.

(5) If we set aside twins with large differences in stature as certainly fraternal, the remainder show that those with large differences in cephalic index have on the average larger differences in stature; *mutatis mutandis*, the same is true of cephalic index. The data thus supply, for the first time, evidence of association of resemblance in different traits.

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A SEX DIFFERENCE IN LINKAGE IN RATS AND MICE

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In a series of experimental studies of heredity in mice and rats, extending over a number of years, DUNN, WACHTER and I thought we had obtained conclusive evidence that crossing over between linked genes occurs more frequently in females than in males; in other words, that the crossover percentage is higher in oögenesis than in spermatogenesis. DETLEFSEN (1925), who has also studied linkage in mice, challenges this conclusion, maintaining that "a significant sex difference occurs in only one set of experiments in mice" and one in rats, the latter being "the best and practically the only unobjectionable evidence of a case of sex difference in crossing over in mammals."

Now, it happens that in every single experiment in which the question of a possible sex difference has been studied, in DETLEFSEN'S own experiments quite as emphatically as in our own, the crossover percentage has always been found to be higher in females than in males, in both mice and rats. DETLEFSEN'S strange skepticism about the matter seems to rest on a peculiar conception of what is and what is not a statistically significant result.

PEARL and MINER (1914) have written on this subject with great clarity and have given us a useful table which shows that at no particular point, such as three times or five times the probable error, does a result suddenly become "significant." Its significance increases steadily as the limits of the probable error are transgressed. A result, which in particular cases scarcely exceeded the probable error, would be full of significance if it occurred *regularly*.

DETLEFSEN'S table 6 summarizes nine different experiments on linkage in mice and rats, some of them made in his laboratory, some in mine. All of these are backcross experiments, the most advantageous form of experiment for the measurement of linkage strength. No experiment includes less than a thousand young; one includes over 30,000. Every experiment shows a *higher percentage* of crossovers among the gametes produced by females than among those produced by males. The difference, as estimated by DETLEFSEN, ranges from 1.2 times the probable error to 7.3 times the probable error. A tenth experiment might be added

to the nine summarized in DETLEFSEN'S table 6, namely, an experiment on the linkage between albinism and red-eyed yellow in rats, wherein over 12,000 young were produced and the crossover percentage was found to be three times as great in females as in males.

It is surely not an accident that all these ten independent experiments have the same qualitative result. All show greater crossing over in females. If we disregard this uniformity and assume that it is due to chance alone, we ascribe to chance something against which the odds are enormous. An event for which the chances are even (greater crossing over in males or in females) would not come out *the same way in ten successive trials*, twice in a thousand times. The odds against it are 520 to 1, according to PEARL and MINER.

But it should be remembered, that even on DETLEFSEN'S conservatively low estimate, the excess of crossovers in oögenesis exceeds the probable error in every case,—in fact, is between once and twice the probable error in five experiments, between twice and three times the probable error in two experiments, exceeds five times the probable error in one experiment, and seven times in another. These are minimum figures, for I am not at all convinced that DETLEFSEN'S peculiar formula for calculating the probable error of a crossover percentage is superior to that commonly in use, which would give lower values for the probable error. DETLEFSEN rightly observes that where one of the two complementary crossover classes is incapable of identification, and is therefore assumed to be equal to the identified one, a possible error is introduced. He meets this by adopting a peculiar method of calculating the probable error. I have met it in a different way by basing the probable error on the half population. If one is not satisfied with this approximation, he can deal simply with the identified crossover class, which should be one-fourth of the whole population, if no linkage exists. If linkage is found, its strength will be measured by its departure from one-fourth of the population, and the probable error will be based on a 3 : 1 Mendelian ratio. Such procedure would be beyond criticism, since only actual observations would enter as data into the calculation and only approved formulae for calculation would be employed. Personally I am satisfied with the simple device of basing the probable error as ordinarily calculated on the half population. I am not willing to accept DETLEFSEN'S round-about method as an improvement on accepted usage.

DETLEFSEN admits that one case for greater crossing over in females is unobjectionable, the one involving pink-eyed yellow and albinism in rats, where the difference exceeds seven times the probable error. But there

are two other cases in rats involving the identically same genes in relation to a third gene, red-eyed yellow. The linkage map for females may be expressed thus:

$$\frac{C \quad 0.5 \quad R \qquad 20.5 \qquad P}{c \qquad\qquad 21.9 \qquad\qquad p}$$

DETLEFSEN admits that the evidence is conclusive for greater crossing over in females in the map region between the genes *C* and *P*. But the gene *R* has been shown to lie between *C* and *P*. Therefore, the regions *CR* and *RP* together cover the entire chromosome region between *C* and *P*. If there is, in the region *CP*, greater crossing over in females than in males (as is admitted by DETLEFSEN), then, there must be more frequent crossing over in one or both of the constituent parts of *CP*, namely, *CR* and *RP*. It will accordingly have to be accepted as certain that either *CR* or *RP* is also "unobjectionably" established as "a case of sex difference in crossing over in mammals." The experimental evidence indicates that in *both* regions crossing over is more frequent in females than in males.

The experiments in mice, as to the relative frequency of crossing over in the two sexes, all have to do with one and the same pair of genes, *C* and *P*, which are possibly homologous with the genes similarly designated in rats, and certainly have a similar somatic expression as well as similar linkage relations. DETLEFSEN presents data based on his own observations, showing that, in a total of 2544 backcross young, female parents gave crossovers more often than males, the difference being 5.8 times the probable error. This, in his summary, he designates a "significant sex difference." If the case is proved by his own experiments, it is certainly not disproved by the previously published observations of others, who obtained the same qualitative results from data several times as great in amount as his own. DETLEFSEN fails to recognize the force of cumulative evidence. I think, accordingly, that the case is fully established for more frequent crossing over in females than in males, at least for that portion of a chromosome which lies between the genes *C* and *P*, both in rats and in mice. Why egg cells and sperm cells show these consistent differences in behavior at maturation remains to be demonstrated.

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POLYPLOID MUTATIONS IN CREPIS. TRIPLOID AND PENTAPLOID MUTANTS OF *CREPIS CAPILLARIS*

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INTRODUCTION

Polyploidy or the increase of the number of basic haploid chromosome sets above the normal double number, is justly attracting the attention of cytologists and geneticists. Besides numerous cases of polyploidy in separate somatic cells, cases are generally known in which all cells composing the organism contain more than two haploid sets of chromosomes. This last category of cases deserves special attention, as this is the simplest form of mutation, yielding itself most easily to investigation.

However, not all described cases of polyploidy are indubitable, as the majority of authors citing them base their conclusions entirely on counting the chromosomes, although it is quite clear, that the counting in itself is insufficient, because the number of chromosomes may increase for other reasons having nothing in common with polyploidy; for instance, from the crossing of species with many chromosomes, or as a consequence of segmentation of the chromosomes, etc. (GATES 1924). Thus, I have proved (NAVASHIN 1925) that in 4- and 5-chromosome species of Crepis there are present new additional chromosomes, not peculiar to a 3-chromosome set, contrary to the established opinion that the "not x-ploid conditions," within the limits of the genus, originate from the repetition of definite chromosomes already contained in the "fundamental" 3-chromosome set of *Crepis capillaris* (L.) Wallr. (=*virens*).

The cases of polyploidy which I have mentioned here are especially interesting in that they do not permit the slightest doubt. Thanks to extremely sharp morphological differences between the chromosomes of

Legend for Plate 1

All the figures were made by means of an Abbé camera lucida, with homogeneous immersion 2 mm objective and compound ocular 18, at the level of the working table.

The ends of chromosomes, turned toward the observer, are schematically represented by white circles.

Figures 1, 2 and 3 belong to the diploid individual; 4, 5 and 6, to the triploid one; and 7 and 8, to the pentaploid one.

In reproduction the original drawings were reduced about 1.5 times.

Fig. 1

Fig. 2

Fig. 3.

Fig. 4.

Fig. 5

Fig. 6.

Fig. 7.

Fig 8.

Crepis capillaris, I could establish with complete certainty, that in the nuclei of triploid and pentaploid mutants there are actually present homologous chromosomes, three of each in the former and five in the latter.

MATERIAL

The material which I have used for my observations was derived from the same specimen (H_5) of *Crepis virens* the caryological study of which has been published in another article (NAVASHIN 1925). The seeds left over from this research were sown in April, 1924, in my seed-plot at Tiflis, and gave 10 individuals which bloomed on the 20th of June and bore abundant fruit. About 150 seedlings, grown from the newly collected achenes, were subjected to a careful caryological study and two polyploid plants were discovered, one triploid and the other pentaploid.

Unfortunately, I could not keep these interesting plants, as they had been destroyed during the fixation of the young roots. But a large stock of seeds, which I am reserving for sowing during the coming spring, will, I hope, give at least several such polyploid individuals. (It is quite improbable that only a single pair of mutants should have occurred accidentally in the first 150 of many thousands of seeds, obtained from one and the same source and under entirely similar conditions.) During the next season I shall sow all the seed I possess for caryologic investigation and the polyploid individuals will, of course, be kept for further study.

The morphology of the cell nucleus of *Crepis capillaris* has been examined in detail in my previous article. It will be sufficient here briefly to characterize it. The normal diploid nucleus (figure 1, plate 1) contains three sharply different haploid chromosomes: one long A-chromosome of two links, one short-capitate C-chromosome and one D-chromosome, supplied with a satellite. These morphological characters of the chromosomes are so constant and clear, that the recognition of the three chromosome forms presented no difficulty in any case.

THE TRIPLOID MUTANT

One of the 150 seedlings appeared to contain constantly nine chromosomes in the cell nuclei of the root-tips. The homologous chromosomes were in threes and, using my previous symbols for different forms of chromosomes, I am designating the nucleus of this mutant thus: 3A, 3C, 3D. In figure 4 can be seen, without further explanation, the triploid composition of the nucleus of this individual; two D-chromosomes are lying obliquely to the plane of section, it is true, but they are unmistakably

recognizable by their satellites; as for the rest, every chromosome can be identified with its homologous chromosome of the normal set, illustrated in figure 1.

In the behavior of the nucleus of this mutant I have observed no peculiarities. The division proceeds entirely normally and I was even able to establish that the satellites, present here in the number of three, arise on the nucleolus just as in the normal (diploid) nucleus, in the prophases. This stage may be seen in figure 5; for comparison the same condition of the diploid nucleus is illustrated in figure 2.

A certain peculiarity is seen in the resting nucleus in that the nucleolus tends to assume a "biscuit-like" shape (figure 6) which suggests the approaching division. In normal (diploid) individuals this has almost never been observed (figure 3).

The dimensions of the nuclei and cells of the described individual are noticeably increased; if the average dimension of the meristem cell of the root of a diploid individual be taken as 1.0, the corresponding dimension in the triploid mutant will be equal to 1.3; and the relation for nuclei (resting) is 1.0 : 1.9. This increase of the size of the root cells is reflected in the enlargement of the whole organ; thus, the root of the triploid individual is considerably thicker than that of the diploid plant.

THE PENTAPLOID MUTANT

This remarkable mutant was discovered in the same material from which the triploid individual originated. In its cell nuclei there were constantly 15 chromosomes, five each of the usual three forms, A, C and D, as shown clearly by figure 7, illustrating the metaphase of the nuclear division of this mutant. The chromosomal formula of this individual is, therefore, 5A, 5C, 5D.

The division of the cell-nuclei in this plant is also entirely normal. The lobulation of the nucleolus, as noted in the resting nucleus of the triploid individual, is here greatly increased. As may be seen from figure 8, illustrating the resting nuclei of the pentaploid mutant, there are nearly always several nucleoli present, or at least, the nucleolus appears elongated, with several interruptions, indicating an approaching breaking up into parts.

The dimensions of the cells and of the nuclei included in them, as well as the dimensions of the whole root, appear greatly enlarged. The cells of the pentaploid mutant exceed those of the diploid individual in average volume 2.5 times, and the resting nuclei appear enlarged 4.1 times.

DISCUSSION

These cases of polyploidy raise a whole line of interesting questions. First of all, a decision must be reached concerning their origin. Generally, it is considered established that polyploidy can arise in two basic ways: one of these may be called vegetative (for instance the polyploid chimera of WINKLER (1910), formed by the fusion of vegetative nuclei in wounded cells); the other may be called generative (GATES 1924). There is no doubt that my described mutants could arise only in the latter way. Two possibilities may be suggested also as to how generative polyploidy may arise: (1) as a consequence of polyspermy; and (2) as a result of a combination of gametes with increased number of chromosomes, as compared with the normal haploid condition. Polyspermy appears to me to be highly improbable, for, although dispermy might possibly occur occasionally (it has never been observed by any one), yet the simultaneous union of more than two sperms with one egg is even less probable. The possibility that four generative nuclei fused with the nucleus of the egg cell, thus giving rise to my pentaploid mutant, cannot, in my opinion, be admitted. The case becomes entirely different, if we assume that these two mutants arose from a combination of gametes containing more than one haploid chromosome set. According to the well-known idea of DE VRIES (1917), I imagine the origin of the triploid mutation to have resulted from the union of a normal, unchanged haploid gamete with a diploid one. That diploid gametes frequently occur in plants is proved by many instances. Besides the "normal" sporogenesis of tetraploid individuals such abnormal gametes may result from an abnormality of the reduction division,—even its complete omission. Such abnormalities of reduction are not rare phenomena, and may be supposed to arise oftenest under the influence of external agencies, probably the most important of which is the temperature, as is indicated especially by the work of DE MOL (1923). By increasing the temperature during the process of pollen formation DE MOL secured diploid pollen grains, and applying this pollen to the stigmas of normal individuals of the same species, he obtained seeds, which gave triploid plants. It is not improbable that in my cultures there prevailed conditions similar to those which were created artificially by DE Mol in his experiments. The Tiflis climate is distinguished by the quick approach of a dry and extremely hot summer; the development of the plants proceeds very quickly, and my plants of *Crepis capillaris*, grown under these unusual circumstances, experiencing a period of accelerated development, probably gave a certain quantity of diploid

pollen. It is perfectly clear that the meeting and combination of two diploid gametes is very much less probable, than the combination of a diploid gamete with a normal haploid one. Thus, the origin of the triploid mutant seems to me sufficiently clear.

It is more difficult to imagine the origin of a pentaploid mutation. The most probable manner of origin of such a mutant, it seems to me, is by the combination of a tetraploid gamete with a normal haploid one. No one has, so far as I know, reported the occurrence of tetraploid gametes, but it is possible to imagine them, theoretically, as a result of non-disjunction of daughter chromosomes after the homeotypic division, if the preceding reduction were omitted, (as during the formation of diploid gametes).

Particular experiments which I have undertaken in this direction will, I hope, explain this question.

However these mutants may have originated, they are of extreme interest for genetics. If they prove to be capable of forming viable gametes, their progeny, thanks to their varied nuclear composition, will give valuable material for research. Based on analogous observations (BELLING 1924), one may think that the extra three chromosomes of our mutants, not finding for themselves homologues, will have to be distributed during sporogenesis, between the daughter nuclei of the diads, in all possible combinations, according to the law of chance. Table 1 includes all kinds of chromosome combinations, which must arise during sporogenesis by triploid and pentaploid individuals.

TABLE 1

Chromosome combinations which must arise during sporogenesis.

TRIPLOID MUTANT			PENTAPLOID MUTANT		
Number of chromosomes	Formula	Extra chromosomes	Number of chromosomes	Formula	Extra chromosomes
3	1A, 1C, 1D		6	2A, 2C, 2D	1A, 1C, 1D
4	2A, 1C, 1D	1A	7	3A, 2C, 2D	2A, 1C, 1D
4	1A, 2C, 1D	1C	7	2A, 3C, 2D	1A, 2C, 1D
4	1A, 1C, 2D	1D	7	2A, 2C, 3D	1A, 1C, 2D
5	1A, 2C, 2D	1C, 1D	8	2A, 3C, 3D	1A, 2C, 2D
5	2A, 1C, 2D	1A, 1D	8	3A, 2C, 3D	2A, 1C, 2D
5	2A, 2C, 1D	1A, 1C	8	3A, 3C, 2D	2A, 2C, 1D
6	2A, 2C, 2D	1A, 1C, 1D	9	3A, 3C, 3D	2A, 2C, 2D

From this table we can see, that both of our mutants must form gametes of 8 different kinds. The triploid mutant will form gametes with different

numbers of chromosomes, ranging from normal haploid up to diploid ones, and the pentaploid from diploids up to triploids.

The progeny anticipated from these mutants would be particularly remarkable. The nuclear composition of all the different zygotes which, according to this theory, must be formed by self-pollination and by crossing with a normal individual, are listed in table 2.

TABLE 2

Chromosome combinations expected in the progeny of two mutants.

TRIPLOID MUTANT						PENTAPLOID MUTANT					
Self-pollination			Crossed with normal			Self-pollination			Crossed with normal		
Number of chromosomes	Number of zygotes	Formula	Number of chromosomes	Number of zygotes	Formula	Number of chromosomes	Number of zygotes	Formula	Number of chromosomes	Number of zygotes	Formula
6	1	2A, 2C, 2D	6	1	2A, 2C, 2D	12	1	4A, 4C, 4D	9	1	3A, 3C, 3D
7	2	3A, 2C, 2D	7	1	2A, 3C, 2D	13	2	5A, 4C, 4D	10	1	4A, 3C, 3D
7	2	2A, 3C, 2D	7	1	3A, 2C, 2D	13	2	4A, 5C, 4D	10	1	3A, 4C, 3D
7	2	2A, 2C, 3D	7	1	2A, 2C, 3D	13	2	4A, 4C, 5D	10	1	3A, 3C, 4D
8	1	4A, 2C, 2D	8	1	2A, 3C, 3D	14	1	6A, 4C, 4D	11	1	3A, 4C, 4D
8	1	2A, 4C, 2D	8	1	3A, 3C, 2D	14	4	5A, 5C, 4D	11	1	4A, 3C, 4D
8	1	2A, 2C, 4D	8	1	3A, 2C, 3D	14	4	5A, 4C, 5D	11	1	4A, 4C, 3D
8	4	2A, 3C, 3D	9	1	3A, 3C, 3D	14	4	4A, 5C, 5D	12	1	4A, 4C, 4D
8	4	3A, 3C, 2D				14	1	4A, 6C, 4D			
8	4	3A, 2C, 3D				14	1	4A, 4C, 6D			
9	2	2A, 4C, 3D				15	2	4A, 6C, 5D			
9	2	4A, 2C, 3D				15	2	4A, 5C, 6D			
9	2	2A, 3C, 4D				15	8	5A, 5C, 5D			
9	8	3A, 3C, 3D				15	2	6A, 4C, 5D			
9	2	3A, 2C, 4D				15	2	6A, 5C, 4D			
9	2	3A, 4C, 2D				15	2	5A, 4C, 6D			
9	2	4A, 3C, 2D				15	2	5A, 6C, 4D			
10	1	2A, 4C, 4D				16	1	4A, 6C, 6D			
10	1	4A, 2C, 4D				16	4	6A, 5C, 5D			
10	1	4A, 4C, 2D				16	4	5A, 5C, 6D			
10	4	3A, 3C, 4D				16	4	5A, 6C, 5D			
10	4	4A, 3C, 3D				16	1	6A, 4C, 6D			
10	4	3A, 4C, 3D				16	1	6A, 6C, 4D			
11	2	3A, 4C, 4D				17	2	5A, 6C, 6D			
11	2	4A, 3C, 4D				17	2	6A, 5C, 6D			
11	2	4A, 4C, 3D				17	2	6A, 6C, 5D			
12	1	4A, 4C, 4D				18	1	6A, 6C, 6D			

From this table it may be seen, that both mutants by self-fertilization must give, according to the usual scheme, zygotes of 27 different kinds,

and consequently, descendants of the triploid mutant will consist of individuals with all kinds of nuclear composition from the normal diploid to the tetraploid; and the descendants of the pentaploid will range from tetraploid up to hexaploid. The most frequent combination (8 in 64, that is, 12.5 percent) in the descendants of both mutants will be again of the parental type,—respectively, triploid or pentaploid. Besides, in the descendants of both mutants there are 8 different homozygotes, which are capable of continuation without segregation.

The greatest interest from the genetic view-point is found in the 7- and 8-chromosome combinations from the descendants of the triploid mutant: 3A, 2C, 2D; 2A, 3C, 2D; 2A, 2C, 3D; 4A, 2C, 2D; 2A, 4C, 2D; 2A, 2C, 4D. If they prove to be viable they should solve an extremely important question about the localization of groups of genes in this or that one of the three chromosomes of the haploid set; such combinations will be extremely rare, but they are especially suitable material for investigating the influence of any definite chromosome on the phenotype.

The next task of my research will be the thorough study of these polyploid mutants, the investigation of their sporogenesis, and the exact cytologic and hybridologic analysis of their progeny.

SUMMARY

1. Among 150 seedlings of *Crepis capillaris* (L.) Wallr. two polyploid mutants were discovered. One was triploid, the other pentaploid. Three sets of three homologous chromosomes, identifiable by their characteristic form, were found in the nuclei of the triploid individual, and three sets of five homologous chromosomes in the nuclei of the pentaploid individual.

2. The hypothesis is proposed that these mutants owe their origin to the unusual climatic conditions under which their parents grew, which influenced the reduction division in such manner that some of the spores (more probably microspores) arose without reduction, thus giving rise to pollen-grains with diploid nuclei. The pentaploid individual is believed to have arisen from the combination of a tetraploid gamete with a normal haploid one.

3. The progenies of these remarkable mutants should be exceptionally favorable objects for genetic research. Among the numerous expected combinations, several should permit a quick solution of the question as to the localization of different groups of genes in this or that one of the three chromosomes of the haploid set in *Crepis capillaris*.

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INHERITANCE OF WHITE PLUMAGE IN PIGEONS

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INTRODUCTION

There are at least four different Mendelian factors which produce white plumage in pigeons and which are inherited independently of each other. In addition to these four factors, there is probably also a large number of modifiers that determine the total amount of white marking, as well as other factors that act independently to produce white plumage. One of the four factors above-mentioned is a dominant factor which in homozygous condition produces a practically self-white bird and in heterozygous condition a nearly white bird. It is typical of the heterozygous dominant white that a large number of individual feathers are partly white and partly colored. The amount of color in heterozygous birds varies from nearly self-white with dark or "stained" beaks, to a large amount of color in the plumage. Young birds of both kinds usually show considerable color in their nest feathers. However, during their first moult the homozygous individuals lose all their color, and the heterozygous young lose a large part of their color. This dominant white in pigeons is very similar, then, to that described by DAVENPORT (1910) in the case of White Leghorn fowls.

The second factor with which this paper deals is a recessive factor for white spotting, similar to the factor discovered by CUÉNOT (1902-1908) in rabbits and mice. Its expression ranges from one white feather, or even none, to self-white, such as is exhibited by most Fantails. In homozygous recessive white-spotted birds the individual feathers are wholly

white or wholly colored, never partly white and partly colored. In heterozygous birds there are often some white feathers, showing incomplete dominance of self-color. These feathers show particularly in the rump, under the tail, near the hocks, and sometimes in the primaries and tail feathers. The variation from very little spotting to self-white is apparently almost continuous. This condition then seems to act in a manner similar to that shown by CASTLE (1911) in the case of the hooded rats.

"Bull"-eye, a condition in which the irises of the bird are a very dark brown, as distinguished from white, red or yellow, is "linked" with the recessive white-spotted condition. "Recessive-white" birds with white eyes are very rare and self-colored birds with "bull" eyes are almost unknown. I have never seen one, although I have been told that they do exist.

The close association between recessive white and "bull" eye furnishes a very handy way of classifying white birds when their genetic makeup is unknown. Dominant-white birds with "bull" eyes are just as rare as "bull"-eyed self-colored.

A third factor for white, also recessive, is the white marking known to fanciers as "mottle," "rose" or "whiteside." It is a common marking appearing in various breeds, but is most common in the Tumbler pigeon. Its expression varies from self-colored or with a few white feathers in the wing butts to what is known as very "gay" whitesides, where the white covers the entire wing except the flights, also the back and rump, the under side of the wings, and occasionally shows also in the neck, tail feathers and flights. It occurs most commonly, possibly exclusively, in red and yellow birds. I have never seen it in blacks, blues, duns or dominant-reds. The condition in blacks, etc., which is known to the fancier as "black mottle," is due to a separate and distinct factor, which is dominant to self-color, and is usually associated with much white in the neck and on the head.

An interesting characteristic that easily distinguishes "mottle white" from the recessive white-spotting factor and from mottle black, is, that in the nest feathers the young red-mottled bird shows absolutely no white feathers, being entirely self-colored; but during the first moult the wing markings appear and the amount of white increases somewhat with every subsequent moult. "Bull"-eyed mottles, either black or red, are unknown.

A fourth factor is that for "mottle black." This factor expresses itself in a manner very similar to the mottle-white factor. However, the young that carry this factor show it from birth, and are never self-colored previous to the first moult, as are birds carrying the "mottle-white" factor.

Birds that are genetically black, never show the "mottle-white" factor, so far as I am aware; but both the blacks and reds can and do show the "mottle-black" factor.

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PREVIOUS WORK WITH WHITE IN PIGEONS

The inheritance of white in pigeons has been discussed frequently and by many investigators, including DARWIN (1868). DARWIN'S experiments were repeated by STAPLES-BROWN (1908) with the help of BATESON. MORGAN (1911) also reports on the inheritance of white color, as do DONCASTER (1911) and COLE (1914).

DARWIN (1868) crossed a black Barb with "a purely bred snow-white Fantail." The offspring were reported as black with a few white feathers, dark reddish brown, and others "snow-white." It is difficult to discuss DARWIN'S results without more particular details as to his matings. He does not state to which generation his various classes of "mongrels" belong, but what he states is perfectly consistent with the results recorded in this paper, if it be assumed that the white Fantail used was a recessive-white bird, the young being expected in this case to be colored, with a few white feathers.

STAPLES-BROWN (1908) attempted to reproduce DARWIN'S experiments. He came to the conclusion that black, blue and red are imperfectly dominant to white. The majority of the first-generation birds produced "show some white feathers, chiefly on the rump." This would be entirely consistent with the supposition that the white Fantails used in his experiments were likewise recessive-white birds. He further made a cross between a white Tumbler with a white eye and a white Fantail with a "bull" eye. From this cross he obtained six pure-white birds and three white with a few colored feathers. In the second generation, by mating together birds showing some colored feathers, he obtained four pure-white birds and six with some colored feathers. He noted that these results were somewhat inconsistent with his conclusions that white is a recessive condition; thus

"The appearance of some colored birds from these matings suggests the possibility that in the white Tumbler, a dominant white factor, comparable with that known in the fowl, may exist."

So far as I know, this is the first suggestion by any investigator that a factor for dominant white may exist in pigeons. His results are entirely consistent with expectation, if the white Tumbler cock used in the experiment was a dominant white and the Fantail hen a recessive white-spotted. Any other explanation does not seem to cover the facts.

DONCASTER (1912) reports a cross between a white Fantail and a red Tumbler giving ten colored young, and showing more or less white markings. Also, a black Fantail with a white Fantail gave thirteen young, all pied, ten having more white than black and three having more black than white. In the reverse experiment, with a white Fantail hen and a black Fantail cock, the young were similar, but with the black and white more nearly equal. Using a second white Fantail hen with the same black Fantail cock, young were produced similar, but with a larger number showing preponderance of white. He then repeated these experiments using other black birds, but obtained approximately the same results.

It is a well-known fact in pigeon breeding that a white Fantail is superior to the colored Fantail in show points. It is very common, therefore, for Fantail breeders to cross their colored birds with white birds in order to improve their quality. For this reason, it is much more likely that a black Fantail should contain recessive white than that a colored tumbler should be heterozygous. DONCASTER'S results can be interpreted by assuming that the Tumbler used was homozygous, giving young that are nearly self-colored with a few white feathers, and that some at least of the black Fantails used were heterozygous for recessive white spotting.

MORGAN (1911) crossed a white Fantail hen with a Blue Swallow and obtained seven young, five pure-white and two with slate-colored feathers. As the Blue Swallow was a white-marked bird, carrying a comparatively small amount of colored feathers, this would be a cross between two recessive white-spotted birds, and, therefore, the results were as expected.

COLE (1914) states that

"As a matter of fact the white pigeon is undoubtedly to be considered as a condition of extreme reduction of spotting." . . . . "This interpretation is borne out by the fact that it is very difficult, if not impossible, to obtain white pigeons which will always produce perfectly white offspring with any color, or foul feathers, as the fancier calls them. I have been told by Tumbler breeders that in their experience there are no white Tumblers which do not occasionally produce offspring with some foul feathers." . . . . "Whether

absolutely true-breeding white varieties occur in other breeds I am unable to say, but I think there is no doubt that in the white Fantail and in the white African Owl there is a much greater tendency for white to come absolutely true."

This explanation does not seem satisfactory. White spotting must have been considered by COLE to be due to a series of dominant factors; otherwise it would be difficult to see how even a few colored feathers could appear in the offspring of pure-white birds. It seems to me that the white Tumbler was a dominant white, and the Fantail and African Owl were recessive white-spotted. This explanation, at any rate, accounts for the different results obtained in breeding whites of these two different kinds. COLE divides the description of the white in the birds bred by him, into seven classifications, as follows: (1) white self; (2) white with a few colored feathers; (3) birds with much color; (4) birds with white and color approximately equal; (5) color in excess of white; (6) self-color except for a few white feathers; (7) self-colored birds with no white feathers. He states, however, that the birds described and divided into these classes were of various ages. Some were described in their nest feathers, some as yearlings, and some as old birds, and it is not specified clearly at what ages the descriptions of the various individuals were taken. It is shown in the present paper that dominant-white birds, even when homozygous, usually display some color in their nest feathers, while recessive white-spotted birds that are self-white when mature are self-white in the nest. Allowing for these differences, the results which he published seem to be consistent with the assumption that the birds used were dominant whites, with the possible complication that some of the self-colored parents were heterozygous for recessive-white spotting. His plates representing the offspring of crosses between self-white and self-red, show individual-feather markings partly white and partly colored, typical of heterozygous dominant-white birds.

EXPERIMENTS INVOLVING DOMINANT WHITE

In the first experiment involving dominant white (table 1) it is to be noticed that all of the six young obtained fell into a class of birds that were nearly all white but showed some colored feathers, as expected. If mottle white were the same factor, then the expectation would have been half white splash and half white self.

In the experiment involving the backcross of the F_1 hen (56) to the dominant-white cock (13) three young were obtained, one self-white and two nearly white. The two birds which had colored beaks and a few

colored feathers were probably to be considered heterozygous; the one with a flesh-colored beak, homozygous.

TABLE 1

Results of the matings involving dominant white.[1]

MATINGS	SELF-WHITE	SPLASH WHITE*	SELF-COLORED	EXPECTATION
Yellow rose (14) × white (13)	0	6	0	0 : 1 : 0
F_1 splash (56) × white (13)	1	2	0	1 : 1 : 0
F_1 splash (60) × splash F_1 (58)	1	4	2	1 : 2 : 1
Dun (33) × splash F_1 (57)	0	2	6	0 : 1 : 1
F_1 splash (59) × kite (19)	0	3	5	0 : 1 : 1
F_1 splash (61) × black (1)	0	4	4	0 : 1 : 1
Splash (231) × splash (233)	1	2	1	1 : 2 : 1
Splash (138) × splash (144)	0	2	0	1 : 2 : 1
F_1 white self (133) × black (1)	0	5	0	0 : 1 : 0
White splash (239) × white (80)	0	2	0	1 : 1 : 0
White (95) × white (80)	5	0	0	1 : 0 : 0
F_2 black self (235) × F_2 dominant red self (235)	0	0	3	0 : 0 : 1
F_2 black self (232) × F_2 dominant red self (236)	0	0	3	0 : 0 : 1

* Including some mottle-white birds.

In the cross between two F_1 birds (60) and (58) two self-colored birds were obtained, which showed no white feathers whatever. This is evidently a clean segregation of recessives. All three classes expected in this experiment were obtained.

The F_2 white self (133) extracted from this cross was mated to the black self cock (1), referred to above; five young were produced, all splashed, making it highly probable that the hen was homozygous for the white factor.

In the three crosses of F_1 birds (57) (59) (61) to self-colored birds (33) (19) (1), the young fell into two classes, white splash, similar to the F_1 parent, and self-colored birds, similar to the recessive self-colored parent.

The cross between the F_1 (61) and black (1) is especially interesting, for the black cock (1) had been bred the previous year to a mottled hen that showed considerable "mottle white." Eight young had been obtained, all of which were pure black, making it very highly probable that the black cock (1) contained no mottle white; while in the cross between the F_1 hen (61) and the black (1) showed four white splash that were very nearly white self. Further tests were made with the young from this

[1] All matings reported in this paper were carried out in single pens.

mating, two pairs of colored selfs from this cross being inbred (sister-by-brother). All of the six young were self-colored, showing no white feathers whatever.

The cross of the F_1 white-splash hen (59) with the kite (19) involved two factors for white: dominant white and mottle white, it being known that both parents were heterozygous for mottle white. The results show independent segregation of these factors, the young being divided into the expected classes as follows: 3 dominant white : 3 self-colored : 2 mottle white.

The cross between the dun hen (33) and the F_1 white-splash cock (57) is very instructive. The cock is known to be heterozygous for dominant white and for mottle white, while the hen is known to be heterozygous for recessive white spotting. If these three conditions were due to the same factor, then the hen would have helped produce a homozygous white bird. This she did not do, the young being two dominant-white splashes and six self-colored birds showing no white, either mottle white or recessive white spotting. The inference is, therefore, that there are at least three separate factors at work here.

Two pairs of F_2 splashes were bred together. One pair produced one white self, two white splashes and one self-colored red. The other pair produced two young only, both splashes.

MATINGS INVOLVING RECESSIVE WHITE SPOTTING

The results of the cross between the yellow self (7) and the Satinette (8) show the dominance of self-color over white-spotted, but also show that this dominance is not absolutely complete, the young showing a few white feathers on the rump. However, the segregation in the F_2 generation is very clean, there being four white-marked young resembling the Satinette grandmother (8) very closely. This proves the recessive nature of white-spotted.

The results obtained in the first generation from the cross between the blue Swallow (70) and the blue Tumbler (71) are very similar to the preceding experiment.

The cross between the blue checker Baldhead (3) and the yellow Rosewing (4) involves two factors: one for recessive white spotting and one for mottle white. The first generation results show the incomplete dominance of self over baldhead marks, and the complete dominance of self over mottle white. In the F_2 generation there is complete segregation, showing the expected classes of baldhead-marked, semi-baldhead, self-color with no white recessive mottles.

TABLE 2

Matings involving recessive white spotting.[1]

MATINGS		NEARLY SELF AND SELF-COLORED	WHITE SPOTTED	RATIO EXPECTED
Blue-laced satinette (8)*	× yellow self (7)	4	0	1 : 0
F_1 dun self (31)	× yellow self (7)	6	0	1 : 0
F_1 dun self (33)	× F_1 black self (30)	8	4	3 : 1
Blue-laced satinette (68)*	× blue check self (63)	2	0	1 : 0
Blue self (71)	× blue barless (70)*	6	0	1 : 0
Yellow rose (4)	× blue check bald (3)	9	0	1 : 0
F_1 black blue-tail (21)	× blue check bald (3)	4	3	1 : 1
F_1 black blue-tail (23)	× F_1 black blue-tail (27)	5	2	3 : 1
F_1 black blue-tail (28)	× F_1 black blue-tail (26)	2	2	3 : 1
Yellow rose (4)	× F_1 black blue-tail (22)	5	0	1 : 0
Red self (79)	× black bald (77)	5	0	1 : 0
Dun self (18)	× red saddle (17)*	2	0	1 : 0
F_1 dun self (64)	× red saddle (17)*	1	1	1 : 1
F_1 black self (65)	× dun-laced self (69)	5	0	1 : 0
F_1 black (223)	× black bald (91)	3	5	1 : 1
F_1 black (220)	× black bald (87)	5	2	1 : 1
F_1 black (222)	× black bald (77)	1	0	1 : 1
Black bald (92)	× F_1 dominant red (221)	3	4	1 : 1
Red self (79)	× F_1 dominant red (219)	5	0	1 : 0
Blue-laced satinette (68)*	× black self (30)	0	1	1 : 1
F_1 silver check (119)	× blue barless (70)*	5	3	1 : 1
Blue bald (179)	× yellow rose (90)	5	0	1 : 0
Yellow rose (206)	× black blue-tail bald (192)	1	0	1 : 0
Blue bald (179)	× almond (249)	3	0	1 : 0
Black (222)	× blue check bald (192)	1	1	1 : 1

		OBSERVED	EXPECTED
Summary	Ratio 1 : 0	61 : 0	61.00 : 0.00
	Ratio 1 : 1	23 : 20	21.50 : 21.50
	Ratio 3 : 1	15 : 8	17.25 : 5.75
	Total	99 : 28	99.75 : 27.25

* These birds had "bull" eyes.

The results obtained from the mating of the red-saddle Fantail (17) with the dun self Fantail (18) are confirmatory in every respect of the preceding matings, there being incomplete dominance in the first generation and complete segregation in the second.

[1] Several different color patterns are included in this table because they all act in the same way when crossed with self-colored birds; and because all of these patterns are associated with "bull" eye.

MATINGS INVOLVING MOTTLE WHITE

TABLE 3

Matings of homozygous black selfs with red mottles (mottle white).

MATINGS		BLACK, NOT-MOTTLE	MOTTLES
Yellow mottle (2)	× black self (1)	9	0
Yellow rose (4)	× blue check bald (3)	9	0
Red rose (6)	× bronze self (5)	3	0
Yellow rose (4)	× bronze self (5)	1	0
Yellow rose (103)	× blue self (84)	3	0
Yellow mottle (204)	× black self (37)	1	0
Blue baldhead (179)	× yellow rose (90)	5	0
Yellow rose (206)	× blue check bald (192)	1	0
		32	0

Table 3 indicates the complete dominance of black self over red mottle (mottle white). When the heterozygous birds were bred together, the results were as shown in table 4.

TABLE 4

MATINGS		BLACK NOT MOTTLE	BLACK MOTTLE	RED SELF	RED MOTTLE
White splash (59)	× kite self (19)	3	0	0	2
Black semi-bald (28)	× black semi-bald (26)	2	0	0	2
Black semi-bald (23)	× black semi-bald (27)	6	0	0	1
Black self (38)	× black self (37)	3	0	0	1
Black self (39)	× black check self (47)	3	0	0	1
Bronze self (153)	× bronze self (149)	4	0	0	0
Total		21	0	0	8
Expected		*16.2*	*5.5*	*5.5*	*1.8*

The eight red-mottles bred show the recessive nature of mottle white to black self.

The backcross of heterozygous cocks to red-mottle hens resulted as shown in table 5.

These results seem to indicate that there is a strong linkage between mottle white and red color. The numbers are too small on which to figure linkage strengths. It seems significant that only five selfs appeared when eleven and one-half were expected and that no black-mottles appeared when eleven and one-half were expected.

Table 6 shows the result of the mating of two heterozygous black cocks with two red self hens heterozygous for mottle white.

TABLE 5

MATINGS		BLACK NOT MOTTLE	BLACK MOTTLE	RED SELF	RED MOTTLE
Yellow rose (14)*	× bronze self (44)	3	0	2	1
Yellow rose (4)	× black semi-bald (22)	1	0	0	4
Red rose (6)*	× bronze self (43)	3	0	3	0
Yellow mottle (2)	× black self (35)	1	0	0	3
Yellow mottle (204)	× black self (37)	1	0	0	0
Red mottle (20)	× kite self (19)	1	0	0	1
Total		10	0	5	9
Expected		*6*	*6*	*6*	*6*

* Hens (14) and (6) are very short rose-wings. Their young may be genetically rose-wing, although they show as self birds.

TABLE 6

MATINGS		BLACK NOT MOTTLE	BLACK MOTTLE	RED SELF	RED MOTTLE
Red self (79)	× dominant red self (219)	3	0	2	2
Yellow self (86)	× bronze self (150)	1	0	1	2
		4	0	3	4

MATINGS INVOLVING MOTTLE BLACK

That mottle black acts differently from mottle white is shown by table 7.

TABLE 7

Results of mating mottle black with self-color.

MATINGS		BLACK SELF	BLACK MOTTLE	RED SELF	RED MOTTLE
Dun mottle (12)	× red self (11)	2	4	0	0
F_1 black mottle (53)	× red self (11)	0	2	1	1
F_2 black mottle (175)	× red self (11)	0	0	0	3
Dun mottle (12)	× F_1 black mottle (54)	0	7	0	0
F_1 black mottle (73)	× dominant red self (46)	2	2	1	1
F_1 black mottle (55)	× bronze self (5)	1	3	0	0
F_2 red self (174)	× F_2 black mottle (167)	0	1	0	1
F_1 black self (72)	× F_1 black self (52)	4	0	1	0

This table shows the dominant nature of black mottle. The mating of the F_1 black selfs is especially to be noted, as it produced self birds only.

The genetic difference between mottle white and mottle black was shown by a mating of kite mottle (139) to red mottle (142). Here two mottle birds were mated together and produced 1 self-colored young with no white feathers whatever, 1 black mottle and 2 red mottle. This, of course, would be impossible if the mottle factors were both recessive and allelomorphic.

SUMMARY

The following are some of the factors that occur in the domestic pigeons. Each seems to be independent of the others, and yet each produces white plumage in the bird affected.

1. "Dominant white," a factor producing, when present in homozygous condition, a white or nearly white bird, and when heterozygous a bird largely white, but always showing an appreciable amount of color.

2. "Recessive white spotting," a factor producing white in a greater or less degree in various parts of the body, varying from self-colored to completely white. This factor is not quite completely recessive to self-colored. In homozygous condition it is almost always associated with dark brown irises.

3. "Mottle white," a recessive factor that has no effect on the nest feathers, but produces a varying amount of white on and under the wings and on the rump in the second coat, and increasing somewhat in amount with each succeeding moult. This factor apparently occurs only in recessive-red birds.

4. "Mottle black," a dominant factor, producing white in varying amounts on and under the wings and on the neck and head.

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